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Systematic Revision of Fossil Prairie Dogs with Descriptions of Two New Species

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INTRODUCTION

Prairie dogs are large North American ground-dwelling squirrels of the genus *Cynomys*, closely related to ground squirrels of the subgenus *Spermophilus* (*Spermophilus*) (Bryant, 1945; Nadler et al., 1971). Two subgenera and five extant species currently are recognized (Pizzimenti, 1975; Hall, 1981). The subgenus *Cynomys*, referred to as black-tailed prairie dogs, includes *C. mexicanus*, today restricted to a small area in northeastern Mexico, and *C. ludovicianus*, which ranges widely across the Great Plains from southern Canada to Texas. The subgenus *Leucocrossuromys* includes three species, collectively termed white-tailed prairie dogs. All three occur on high-elevation basins or plateaus associated with the Rocky Mountains. *Cynomys gunnisoni* inhabits the southern Rockies; *C. parvidens*, in southwestern Utah, and *C. leucurus*, in the central Rockies and Wyoming Basin, form a closely related pair of allospecies (Pizzimenti, 1975). The terms "black-tailed," "black tails," "white-tailed," and "white tails" will be used frequently in this paper to refer to the respective subgenera.

Cynomys is known in the fossil record from the Late Pliocene (Late Blancan) to Holocene. The first fossil species to be described was *C. niobrarius* (Hay, 1921). Five additional fossil species have since been named (*C. vetus* Hibbard, 1942; *C. meadensis* Hibbard, 1956; *C. spispiza* Green, 1960; *C. hibbardi* Eshelman, 1975; *C. churcherii* Burns and McGillivray, 1989). Fossils have also been referred to three extant species (*C. ludovicianus*, *C. leucurus*, *C. gunnisoni*). Thus, nine prairie dog species have been recognized in the fossil record. Lacking a comprehensive review, the systematics of fossil *Cynomys* has become confused.

The primary purpose of this paper is to revise the systematics of fossil prairie dogs. In doing so, it is necessary to revise the diagnoses of the genus and two subgenera, and for these purposes I examined samples of all extant species. Extant species, however, are only treated in species accounts if preserved as fossils. I also consider the phylogenetic relationships among fossil and Recent species of *Cynomys*.

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MATERIALS AND METHODS

For this revision, I examined over 400 fossil (pre-Holocene) prairie dog specimens and Recent samples of five extant species. My study focussed on lower jaws with teeth because they are abundant and diagnostic as fossils. Relatively complete skulls, uncommon as fossils, were considered when available. Isolated teeth were only utilized when other, more complete specimens were rare or absent at a locality. Post-cranial elements were not studied.

Cranial and dental descriptions and comparisons of Recent prairie dogs have been provided by Hollister (1916) and Bryant (1945). Using characters listed in these sources as a starting point, I made detailed comparisons among fossil and Recent forms. Special attention was given to qualitative morphological descriptions in accounts of the genus, species of uncertain subgenus, and the subgenera. Differentiation among species within each subgenus was based primarily on quantitative features. Features of external and soft anatomy, biochemistry, genetics, and ecology are taxonomically useful for Recent species (Hollister, 1916; Tileston and Lechleitner, 1966; Nadler et al., 1971; Pizzimenti, 1975 and references therein; Hoogland, 1981; McCullough et al., 1987). These features, however, were not treated in this revision because they cannot be evaluated on fossil forms.

AGE DETERMINATION

The chronologic scheme used herein is the Land Mammal Ages proposed by Wood et al. (1941) and subdivided by Schultz et al. (1978). A recent review of Plio-Pleistocene Land Mammal Ages is provided by Lundelius et al. (1987). Fossil prairie dogs are known from the following intervals: Senecan (Late Blancan; ca. 2.5–2.0 my B.P.); Sappan (Early Irvingtonian; ca. 2.0–0.75 my B.P.); Cudahyan (Medial Irvingtonian; ca. 0.75–0.50 my B.P.); Sheridanian (Late Irvingtonian; ca. 0.50–0.20 my B.P.); and Rancholabrean (0.20–0.01 my B.P.). The last was further subdivided herein into Early (Late Illinoian and Sangamonian; ca. 0.20–0.10 my B.P.) and Late Rancholabrean (Wisconsinan; ca. 0.10–0.01 my B.P.). Some fossils could not be placed more precisely than Sheridanian or Early Rancholabrean; I use the term Illinoian to refer to this interval. Abso-

lute age estimates given above are based on previous correlations of faunas with dated stratigraphic sequences.

In general, I considered fossil *Cynomys* to have approximately the same age as associated fauna and sediments. Dating a fossil usually was based on the age of the associated fauna or sediment as estimated by some combination of biostratigraphic, lithostratigraphic, paleomagnetic and radiometric evidence. In some cases, I estimated age based on the prairie dog fossils themselves (Goodwin, 1993). Details about specific lines of evidence used in the chronological placement of individual localities are provided elsewhere (Goodwin, 1990a:281 and references therein; modified as in Goodwin, in prep.).

Because prairie dogs are burrowing rodents, their fossils may be younger than the sediments and faunas in which they occur. If the age of a fossil was suspected by the original collector, or if state of preservation or stage of evolution was out of character with associated fauna, I eliminated the specimen from my analysis. Nonetheless, some fossils considered herein probably are unrecognized intrusives.

TERMINOLOGY AND MEASUREMENT PROTOCOL

Cranial and mandibular terminology generally follow Bryant (1945); dental terminology follows Wood and Wilson (1936).

Table 1 lists and briefly describes the cranial and mandibular variables that I measured. Many are not standard measurements taken in studies of Recent skulls. I selected variables based on the frequency of preservation on fossils and probability of systematic usefulness (based on previous studies or my own observations). I took measurements with a dial calipers.

Table 2 lists and briefly describes the dental variables that I measured. All dental measurements were taken with a Daedal combination linear/rotary measuring stage under an Olympus binocular dissecting scope. Dental measurements represent measures of the tooth in occlusal view. Because of the shape of *Cynomys* cheek teeth, slight buccal or lingual rotation may result in somewhat different measures of width. I was unable to find absolute criteria for orientation, but the following protocol minimizes variability due to orientation.

Table 1. Description of cranial and mandibular measurements taken in this study.

Variable	Description
PALM ³	Width of palate between lingual borders of M ³ alveoli
PALP ³	Width of palate between lingual borders of P ³ alveoli
MXALV	Length of maxillary alveolar row parallel to its long axis
PALLN	Length of palate from notch in premaxillae above the I ¹ alveoli to the anterior margin of the left or right internal nares
SKLN	Length of skull from notch in premaxillae above the I ¹ alveoli to the anteroventral border of the foramen magnum
INTOR	Least width of the interorbital region, including the supraorbital notches (if developed)
PSTOR	Post orbital width immediately posterior to the postorbital processes
OCCPW	Width of occiput across the paroccipital processes
OCCPH	Height of occiput from base of the medioventral wall of the foramen magnum to the dorsalmost point of the occiput
FORMW	Greatest width of the foramen magnum
FORMH	Greatest height of the foramen magnum
EAML	Greatest anteroposterior dimension of the external auditory meatus
MDALV	Length of mandibular alveolar row parallel to its long axis
ANTJW	Length of anterior part of jaw from posterior border of alveolar row to dorsoposterior margin of the I ₁ alveolus

P³—Tooth oriented with the single root projecting directly away from the viewer.

P₄—M³—Tooth oriented with the three roots projecting away from the viewer at approximately equal angles. This was usually easy to determine, less so on M³, thus measures of width on the latter may be less repeatable.

P₄—Proper orientation usually about halfway between two limits defined in the rotation of P₄ around the anteroposterior axis of the jaw, namely that point in lingual rotation where the tip of the metaconid extends beyond the lingual margin of the trigonid, and that point in buccal rotation where the posterolingual root becomes visible below the lingual margin of the talonid.

M₁—M₃—Tooth oriented such that the two anterior roots project away from the viewer at approximately equal angles relative to the

line of sight. The direction of root projection usually could be estimated from the exposed proximal portion. In some cases, roots were not readily visible, and orientation was estimated based on experience gained from measuring numerous teeth.

MORPHOMETRIC METHODS

It usually was difficult to distinguish among fossil and Recent prairie dogs within a subgenus based on qualitative dental features. Taxonomic decisions at this level were dependent heavily on morphometric evidence.

Selection of operational taxonomic units and samples.—For each subgeneric analysis, operational taxonomic units (OTUs) included all Recent species and putative fossil forms (delimited temporally and/or geographically) assignable to that sub-

Table 2. Description of dental measurements taken in this study. See text for orientation criteria.

Variable	Description
LP ³	Greatest length of P ³ perpendicular to long axis of protoloph.
WP ³	Greatest width of P ³ parallel to long axis of protoloph.
LP ⁴ , LM ^x	Greatest length of indicated upper tooth perpendicular to long axis through trigon.
WP ⁴ , WM ^x	Greatest transverse width of indicated upper tooth parallel to long axis through trigon.
LP ₄ , LM _x	Greatest length of indicated lower tooth perpendicular to long axis through trigonid.
WTRP ₄	Greatest transverse width across the trigonid of P ₄ parallel to the long axis of trigonid.
WTLP ₄	Greatest transverse width across the talonid of P ₄ parallel to the long axis of trigonid.
WM _x	Greatest transverse width across trigonid of indicated lower molar parallel to the long axis of the trigonid.

genus. Fossil OTUs do not correspond with named fossil species for black tails but do for white tails. Samples of fossil OTUs are the pooled minimum number of individuals (MNI) from relevant (appropriate age and/or geographic location) fossil localities. To avoid circularity, fossil localities dated on the prairie dogs themselves (Goodwin, 1993) are not included in the samples of temporally-defined OTUs.

Principal component analysis.—I used correlation-based principal component analysis (PCA) to summarize size and shape variation among fossil and Recent OTUs within each subgenus. PCA is a multivariate technique designed to reduce the number of variables that need to be considered from many correlated variables to a few uncorrelated ones (called the principal components) that are linear combinations of the original variables (Manly, 1986). I used the SAS statistical package (SAS, 1985) to perform PCA.

My interpretation of a principal component was based on the correlations (termed loadings) of the original variables with that component. If all loadings were high and positive, I interpreted that component as a general size axis (frequently the first principal component, PC1). If some loadings were high and positive whereas others were high but negative, I considered that component as a shape axis [contrast between variables with positive and negative loadings; frequently principal component two (PC2) and following].

Separate PCAs were performed on cranial data from each subgenus. Fossil skulls usually are dam-

aged, thus only a subset of the original variables was used in each cranial PCA in order to increase sample size. PCAs also were performed on lower dental data. For the subgenus *Leucocrossuromys*, a single analysis was done using a set of 7 dental variables (measurements of P₄–M₃). For the subgenus *Cynomys*, separate analyses were done using anterior (P₄–M₁) and posterior (M₂–M₃) dentition, respectively.

Statistical comparisons.—I made comparisons among fossil and Recent OTUs within each subgenus using as variables the first two axes (PC1, PC2) of the cranial PCA (for *Leucocrossuromys* only); alveolar length (MDALV); and PC1 and PC2 of each dental PCA. Principal components were used as variables because they generally summarize variation in size (PC1) and aspects of shape (PC2). Each variable was tested for normality within each sample using the Kolmogorov-Smirnov test (test statistic derived by the BASTAT routine of the BIOM statistical package; Rohlf, 1985) and for homogeneity of variances among samples using the F-max test. Unless noted otherwise, these assumptions were found to be valid. I used the MCPAIR routine of BIOM (Rohlf, 1985) to make statistical comparisons among sample means.

PHYLOGENETIC ANALYSIS

I investigated phylogenetic relationships among Recent and fossil prairie dogs using the computer program PAUP (phylogenetic analysis using parsimony).

mony; Swofford, 1985). I treated characters as ordered and employed the branch and bound algorithm to find all equally parsimonious phylogenetic hypotheses. These hypotheses were rooted using a hypothetical ancestor based on the shared morphology of *Spermophilus richardsonii* and *S. parryi*, one or both of which usually were placed as or within the sister group of *Cynomys* in phylogenetic hypotheses generated in a preliminary study of relationships among species of the subgenus *Spermophilus*—genus *Cynomys* clade (Goodwin, 1990a). For each hypothesis, PAUP generated a consistency index which is the theoretical minimum number of evolutionary steps divided by the actual number of steps.

ABBREVIATIONS

Variables.—Abbreviations of cranial and dental variables are given in Tables 1 and 2.

Institutions and collections.—Material pertinent to this study was obtained from numerous institutions and collections. The following abbreviations are found in the text, figures, tables, and appendix:

ADAM—Adams State College, Alamosa, Colorado
 AMNH—American Museum of Natural History, New York
 DMNH—Denver Museum of Natural History, Denver
 FHSU—Sternberg Memorial Museum, Fort Hays State University, Hays, Kansas

IMNH—Idaho State University, Museum of Natural History, Pocatello
 IOWA—University of Iowa, Iowa City
 KUM—Natural History Museum, University of Kansas, mammalogy collection, Lawrence
 KUVF—Natural History Museum, University of Kansas, vertebrate paleontology collection, Lawrence
 MWU—Midwestern University, Wichita Falls, Texas
 PMA—Provincial Museum of Alberta, Edmonton
 ROM—Royal Ontario Museum, Toronto
 SMU—Southern Methodist University, Dallas
 SDSM—South Dakota School of Mines, Geology Museum, Rapid City
 TMM—Texas Memorial Museum, University of Texas, Austin
 TTU—The Museum, Texas Tech University, Lubbock
 UCM—University of Colorado Museum, Boulder
 UMMP—University of Michigan Museum of Paleontology, Ann Arbor
 UMTG—University of Montana, Geology Museum, Missoula
 UNSM—University of Nebraska State Museum, Lincoln
 USG—University of Saskatchewan, Department of Geology, Saskatoon
 USNM—United States National Museum, Washington
 UTEP—University of Texas, El Paso
 UWYA—University of Wyoming, Anthropology Museum, Laramie
 UWYG—University of Wyoming, Geology Museum, Laramie

SYSTEMATIC ACCOUNTS

ORDER RODENTIA

FAMILY SCIURIDAE

Genus *Cynomys*

Figures 1A, 1C, 1E, 1G

Synonymy.—Summarized by Hollister, 1916:10, and Hall, 1981:410, for Recent forms.

Type Species.—*Cynomys socialis* Rafinesque, 1817 (= *Cynomys ludovicianus*).

Geologic and Geographic Range.—Late

Blancan (Senecan) to Recent; restricted to a zone from northern Mexico to southern Canada across mid-continental North America.

Emended Diagnosis.—Large ground squirrels resembling the subgenus *Spermophilus*, but with relatively larger cheek teeth; maxillary tooth rows strongly convergent posteriorly; protolophid of P_4 complete or nearly so and well developed; metalophid of M_3 complete, merges lingually with posterior wall of trigonid well up from floor of talonid.

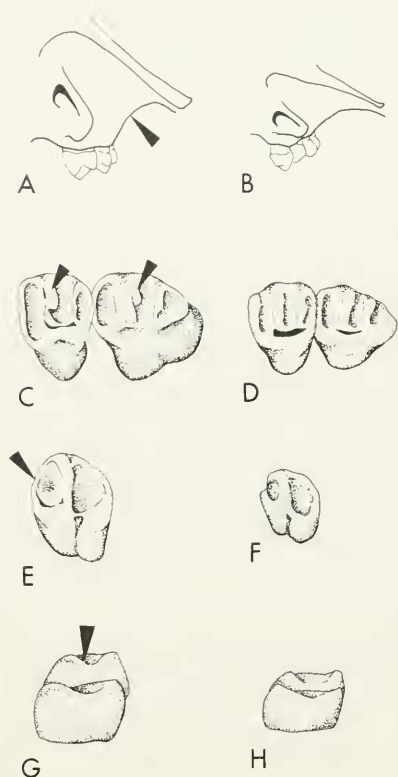


Fig. 1. Comparisons of the genus *Cynomys* (A, C, E, G) with the large ground squirrel, *Spermophilus parryi* (B, D, F, H). (A–B) Anterior view of L maxilla; (C–D) occlusal view of LM²–M³; (E–F) occlusal view of LP₄; (G–H) posterior view of LM₃. Arrows point to generic characters noted in text.

DESCRIPTION

Skull.—The skull of *Cynomys* is robust, more so than is typical for other ground squirrels. In dorsal view, the skull resembles the subgenus *Spermophilus* in that the rostrum has subparallel sides, the interorbital and postorbital widths are subequal, and the zygomatic arches are expanded, especially at the squamosal roots.

The maxilla and palate exhibit several distinctive features. The infraorbital foramen is strongly triangular, the lateral wall sloping ventrolaterad, resembling advanced members of the subgenus *Spermophilus*. The basal (ventral) wall of the foramen usually is robust and inclined, sloping lateroventrad from its medial end (Fig. 1A); in the subgenus *Spermophilus* this margin is more slender and usu-

ally horizontal in orientation (Fig. 1B). The masseteric tubercle typically is massive, positioned at the ventrolateral corner of the foramen, and laterally extended.

The zygomatic plate of the maxilla, in anterior view, is deeply concave along its ventral margin in advanced species of *Cynomys* (Fig. 1A); in ground squirrels this margin is less deeply concave (Fig. 1B). The alveolar rows on each side of the palate are strongly convergent posteriorly in most specimens. In a few specimens of ground squirrels, I have noted weak posterior convergence but never as strongly as is typical for *Cynomys*.

Upper dentition.—The upper incisors are robust and procumbent. The upper cheek teeth, as well as the lowers, are large relative to skull size, and extremely hypsodont in advanced fossil and extant species. In this respect, prairie dogs differ from all known fossil and living ground squirrels. Extreme hypsodonty is especially evident lingually at the protocone. Several early prairie dogs have less hypsodont teeth, resembling large advanced ground squirrels; the extreme hypsodonty evident today developed since the origin of the clade.

P₃ is large; is usually somewhat flattened anteriorly; and bears a high, functional protoloph. P₄–M₂ are triangular in occlusal view, as in the subgenus *Spermophilus*, but are relatively wider. On M₁–M₃, the buccal one-half of the protoloph frequently is expanded along its posterior margin, approaching an accessory lophule on M₃ (Fig. 1C; contrast with Fig. 1D). The expanded section of the protoloph is terminated lingually by a sharp indentation from the posterior direction (Fig. 1C). In morphologically derived prairie dogs, M₃ is long relative to M₂; early prairie dogs appear to have a much shorter M₃. The metaloph on M₃ is well developed and extends all the way across the tooth.

Lower jaw and dentition.—The portion of the lower jaw beneath the diastema is robust and short relative to the length of the jaw. The mental foramen typically is positioned somewhat anterior to the plane of the anterior root of P₄, more anteriorly than usual for many members of the subgenus *Spermophilus*. The coronoid process projects strongly dorsad, and the angular process turns inward at an angle of about 90° to the plane of the posterior part of the ramus, in both respects resembling the subgenus *Spermophilus*.

?Cynomys vetus Hibbard, 1942

Figures 2A–D, 3A

Cynomys vetus Hibbard, 1942:268.

Holotype and Only Specimen.—KUV 6187, fragmentary skull including palate with right and left P₃–M₃, isolated right and left I¹, and parts of skull roof, squamosal, and jugal of a mature to old adult.

Horizon and Type Locality.—Probably Late Blancan (Senecan); reported from the “Early phase of the Loveland loess (brown zone, whitened by calcareous matter and containing large limestone concretions, occurring below the typical red phase)” (Hibbard, 1942:268); unnamed locality, Sec. 3, T. 1 S., R. 10 W, Jewell County, Kansas. It should be noted that these deposits are clearly not equivalent with the Loveland as the term is usually used (Illinoian complex of loesses and paleosols; Schultz and Martin, 1970).

Geologic and Geographic Range.—Known only from the type locality.

Emended Diagnosis.—Smaller than all extant *Cynomys*; distinguished from all extant and fossil species known from appropriate material by relatively shorter M₃, more circular P₃, more concave anterior margin of the squamosal arm of zygomatic arch (anterodorsal view), less concave ventral margin of zygomatic plate (anterior view).

DESCRIPTION

The following cranial measurements were obtained or estimated from the type: INTOR, 9.4 mm; PSTOR, 12.7 mm (both are estimates made on reconstructed skull roof); MXALV: left, 14.55 mm; right, 13.65 mm. Dental measurements are given in Table 3.

Skull roof.—The skull roof is incompletely preserved, but it was possible to reconstruct the outline of a portion thereof by projecting a mirror image of the preserved fragment (Fig. 2A). The suture between the frontals and the nasals and right premaxilla is preserved (Fig. 2A). The premaxilla does not extend posteriad beyond the nasals as it does in many specimens of *Cynomys gunnisoni*. The interorbital width of the frontals, as reconstructed in Fig. 2A, is less than the postorbital width. The supraorbital notches are well developed and deep,

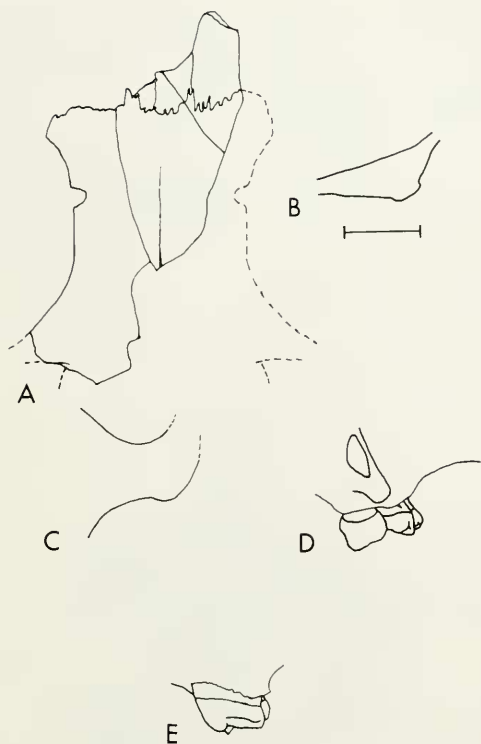


Fig. 2. (A–D) Holotype of *Cynomys vetus* (KUV 6187): (A) dorsal view of preserved and partially reconstructed skull roof (reconstruction shown as dotted line); (B) lateral view of R jugal angle; (C) anterodorsal view of squamosal root of zygomatic arch; (D) anterior view L maxilla. (E) Anterior view of L maxilla of *C. sappaensis* (UNSM 11761). Scale bar represents 5 mm.

P₄ usually exhibits a complete, well developed protolophid (Fig. 1E); the protolophid is variably developed in other ground squirrels, but when prominent is separated from the metaconid by a distinct notch (Fig. 1F). M₁–M₂ bear a complete metalophid, particularly developed in advanced species. The talonid of these two teeth, when unworn, typically bears a lophid or one or more developed cusplids, but these structures frequently disappear with moderate tooth wear. Similar structures seldom are found in the subgenus *Spermophilus*. M₃ exhibits a complete metalophid on all prairie dogs (Fig. 1G; contrast with Fig. 1H), but it is not as strongly developed in early forms. The talonid bears a deep to very deep basin trench along the lingual border of the ectolophid, much more developed than in any extant species of *Spermophilus*.

Table 3. Measurements of upper dentition for three fossil prairie dogs.

Variable	? <i>C. vetus</i> KU 6187	<i>C. sappaensis</i> UNSM 11761	<i>C. spenceri</i> UNSM 33798
LP ³	2.83	—	3.02
WP ³	3.02	—	3.50
LP ⁴	3.04	—	3.20
WP ⁴	4.29	—	4.52
LM ¹	2.64	2.87	3.08
WM ¹	4.68	4.61	4.75
LM ²	2.78	2.84	3.06
WM ²	4.55	4.43	4.66
LM ³	3.16	—	4.04
WM ³	4.27	—	4.25

more so than on most prairie dogs but within the range of variation exhibited by the genus. The base of the left postorbital process suggests that it was moderately robust.

Jugal.—The jugal angle of the zygomatic arch, in lateral view, is relatively triangular in shape, capped ventrally by a distinct apical prominence (Fig. 2B). The arm of the jugal extending posteriad from the triangle tapers gradually; it does not thin rapidly into a thin sheet as in the subgenus *Leucocrossuromys*. In these respects, *Cynomys vetus* resembles the subgenus *Cynomys*, although the jugal is even more triangular in the latter.

Squamosal.—The anterior margin of the squamosal root of the zygomatic arch, viewed anterodorsally, is strongly concave (Fig. 2C), not flattened as in many prairie dogs. The posterolateral portion of the squamosal root is not extended as strongly posteriad as in many prairie dogs. Viewed laterally, the portion of the squamosal ventral and posterior to the root of the zygomatic arch and anterior to the auditory bulla extends more posteriad relative to the position of the root than it does in any other *Cynomys* specimen that I examined.

Maxillae and palate.—The infraorbital foramina are moderately large, triangular. The masseteric tubercles are moderately developed but not strongly directed laterally. Viewed anteriorly, the ventral margin of the zygomatic plate of the maxilla is weakly concave and merges gradually with the border of the alveolar row (Fig. 2D), not strongly concave as in other *Cynomys* for which this charac-

ter is known (Fig. 1A). Viewed ventrally, the zygomatic notches terminate opposite M¹, not M² as appears to be suggested in the original description (Hibbard, 1942:268).

The palate appears narrow (Fig. 3A), at least in part because the tooth rows were rotated ventro-medial around the palatal midline when the fossil was originally prepared and glued together. Allow- ing for this distortion, the palate still would probably be narrower than typical for ground squirrels of the subgenus *Spermophilus* and most specimens of prai-

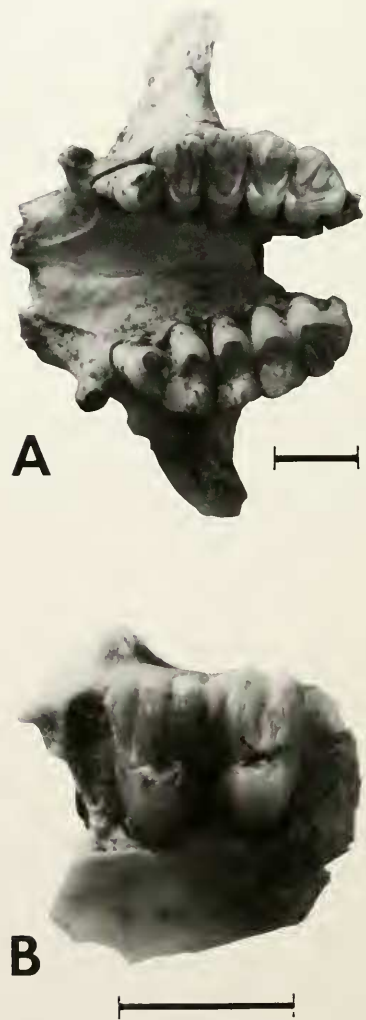


Fig. 3. Occlusal views of: (A) holotype of ?*Cynomys vetus* (KUVP 6187); (B) L maxilla with M¹–M² referred to *C. sappaensis* (UNSM 11761). Scale bars represent 5 mm.

rie dogs. The tooth rows converge posteriorly, more strongly than in *Spermophilus*. Lengths of right and left alveolar rows differ significantly due to the strong anterodorsad direction of the root on left P³.

Upper dentition.—The incisors are strongly curved and relatively deep for the size of the specimen. The cheek teeth are heavily worn, and details of cusp and loph morphology are largely obliterated.

P³ is large and rounded, lacking the anterior flattening typical for advanced prairie dogs. The ridge bounding the anterior cingulum appears low, not as well developed as in the subgenus *Cynomys*. P⁴–M² are triangular in occlusal outline. All three of these teeth exhibit a developed, buccally extended parastyle. The parastyle and metacone both extend more buccad than does the paracone, thus the buccal margins appear indented at the paracone, especially on M¹. M³ is much shorter relative to the length of M² than in other prairie dogs or advanced members of the subgenus *Spermophilus*. Although worn, M³ appears to have had a developed metaloph.

COMMENTS

The large P³ and triangular upper cheek teeth exhibited by ?*Cynomys vetus* support a relationship with the advanced ground squirrel clade which includes *Cynomys* and the subgenus *Spermophilus*. The posteriorly convergent tooth rows support a relationship with *Cynomys*, and the conformation of the jugal angle exhibited by the fossil is similar to (but not as well developed as) the subgenus *Cynomys*. This is consistent with Hibbard's original suggestion that ?*C. vetus* was a member of the latter (Hibbard, 1942).

However, ?*Cynomys vetus* lacks a number of derived features characteristic of the subgenus *Cynomys* or even of the genus. In contrast with the subgenus *Cynomys*, the fossil lacks the extreme development of the anterior cingular ridge on P³. In contrast with all other known prairie dogs, the fossil lacks apparently derived features of the P³, M³, conformation of the squamosal, and conformation of the zygomatic plate (see the description for details). In these respects, ?*C. vetus* is more similar to ground squirrels of the subgenus *Spermophilus*. In at least one feature—the short M³—the fossil appears to be even less derived than many extant species of the subgenus *Spermophilus*. This sug-

gests that some of the advanced features characteristic of both *Cynomys* and *Spermophilus* arose in parallel, unless morphologically derived species of the subgenus *Spermophilus* are more closely related to *Cynomys* than is ?*C. vetus*.

I follow Hibbard (1942) in assigning *vetus* to the genus *Cynomys*, but I query the assignment because of the uncertainty noted previously. The fossil is either a primitive prairie dog or a ground squirrel convergent on the prairie dog morphotype. I doubt that it has special relationship with the subgenus *Cynomys*, thus I regard the similarity of jugal conformation as convergence. Alternatively, the triangular jugal may be a primitive state retained by the subgenus *Cynomys*. However, this interpretation is not supported by outgroup comparisons—ground squirrels lack a strongly triangular jugal.

The relationship between ?*Cynomys vetus* and other fossil prairie dogs deserves attention. It is small and primitive as is *C. hibbardi*, but the latter is known only from a lower jaw with teeth. Relative sizes of M³ and M³ are usually correlated in ground-dwelling squirrels. Assuming this correlation to be true for these forms, ?*C. vetus* had shorter posterior molars than did *C. hibbardi*. This suggests that ?*C. vetus* was the more primitive of the two.

M¹–M² of the fossil resemble in general shape and size those of a small prairie dog from the Sappa Local Fauna, described herein as a new species. Detailed dental comparisons are not possible because of the extreme wear on ?*Cynomys vetus*, but the conformation of the ventral margin of the zygomatic plate on the Sappa form is clearly prairie dog-like and differs from the condition seen in the type of ?*C. vetus*.

Dalquest (1967) referred prairie dogs from the Slaton Local Fauna of Texas to *Cynomys vetus* and suggested that they represented a white tail. The Slaton prairie dogs are relatively small and P⁴–M² are roughly comparable in size with the type of ?*C. vetus*. However, subsequent work showed that the Slaton specimens represent an advanced black tail (Dalquest, 1988) with no relationship to ?*C. vetus*.

Eshelman (1975) referred associated left and right lower jaws from the White Rock Local Fauna to ?*Cynomys vetus* based on size. The absence of cranial and upper dental elements makes this assignment uncertain. The jaws are robust; the mental foramen is positioned far forward; and P₄ appears to

exhibit a complete protolophid (descriptions and fig. 4C–D in Eshelman, 1975). These characters are consistent with assignment to *Cynomys*. However, the metalophid on M_2 – M_3 is incomplete, removing the specimens from *Cynomys* as diagnosed herein.

Cynomys hibbardii Eshelman, 1975

Figures 4A, 4C–D

Cynomys hibbardii Eshelman, 1975:27.

Holotype.—UMMPV61648, left lower jaw with M_1 – M_3 .

Horizon and Type Locality.—Late Blancan (Senecan); collected “at UM-K9-72 in the silty clay lithosome, approximately 2.2 m below the contact with the sand lithosome, Belleville Formation, SE1/4, SE1/4, SW1/4, Sec. 34, T. 1 S, R. 5 W, Republic County, Kansas” (Eshelman, 1975:27).

Referred Specimen.—UMMPV74510, unworn right M_2 , from Nash Local Fauna, Meade County, Kansas.

Geologic and Geographic Range.—Known from the Late Blancan (Senecan) and Early Irvingtonian (Sappan) of Kansas.

Emended Diagnosis.—*Cynomys*, but smaller than all extant species; teeth less high crowned than other fossil and Recent species, possibly excepting ?*Cynomys vetus*; metalophid complete on M_1 – M_2 but deeply notched; metalophid complete on M_3 but less well developed than in other species.

DESCRIPTION

Lower jaw.—Selected measurements of the lower jaw and dentition are provided in Table 4. A lateral view of the holotype is given in Figs. 4A. The portion of the jaw beneath the diastema is similar in proportion to other prairie dogs, but is shorter and more robust than typical for ground squirrels of the subgenus *Spermophilus*. The position of the mental foramen—somewhat anterior to the plane of the anterior root of P_4 —also resembles other *Cynomys* rather than *Spermophilus*. The symphyseal region of the jaw, viewed dorsally, is shorter anteroposteriorly than in any other prairie dog specimen that I have examined for this character. The masseteric ridge is well developed ventrally; the anterior limit of the masseteric fossa lies at the level of the posterior half

of P_4 . The condyloid process is relatively longer and less robust, and bears a relatively deeper fossa on its lateral surface, than is typical for extant *C. ludovicianus* and *C. leucurus*, but these features resemble some specimens of *C. gunnisoni*.

Lower dentition.—An occlusal view of the cheek teeth of the holotype is given in Fig. 4C. I_1 and P_4 are missing, but the preserved alveoli suggest that the former was rather robust and that the latter was relatively long with a single, transversely expanded anterior root. M_1 – M_3 are relatively narrow transversely and exhibit an anterior bulge of the protolophid, but in both respects are within the range of variation exhibited by extant prairie dogs. M_1 – M_2 both exhibit a complete, but deeply notched, metalophid which forms an incomplete posterior boundary to the anterobuccally-posterolingually oriented trigonid basin. The talonid basin of these teeth is rugose, especially on M_2 where the rugosity forms a distinct, transversely oriented lophid running from the base of the entoconid toward the base of the hypoconid. This lophid is particularly high in an unworn specimen from the Nash Local Fauna (Eshelman and Hibbard, 1981) referred here to *C. hibbardii* (UMMP V74510; Fig. 4D). On both M_1 and M_2 , the rugose portion of the talonid is separated from the well developed ectolophid by a deep trench.

M_3 is elongate relative to the M_2 , much as in other prairie dogs. Its trigonid resembles M_1 – M_2 in most respects. The metalophid is slightly less developed but is complete, merging with the posterolingual wall of the trigonid about half-way up from its base. In most ground squirrels, even advanced forms of the subgenus *Spermophilus*, the metalophid projects towards the floor of the talonid basin and only joins the posterolingual wall of the trigonid, if at all, near its base. The talonid of M_3 bears a low, rugose ridge which, from a point just posterior to the metaconid, arches buccad and slightly posteriad toward the ectolophid, and then posteriad and slightly linguad until it merges with the posterolophid. This ridge is separated from the ectolophid by a well developed trench, but the trench becomes very narrow near its midpoint. There is no bridge connecting the ectolophid and talonid. The hypoconid is strongly deflected anteriorly, and there is no ectostylid in the hypoflexid, in both respects resembling black-tailed rather than white-tailed prairie dogs.

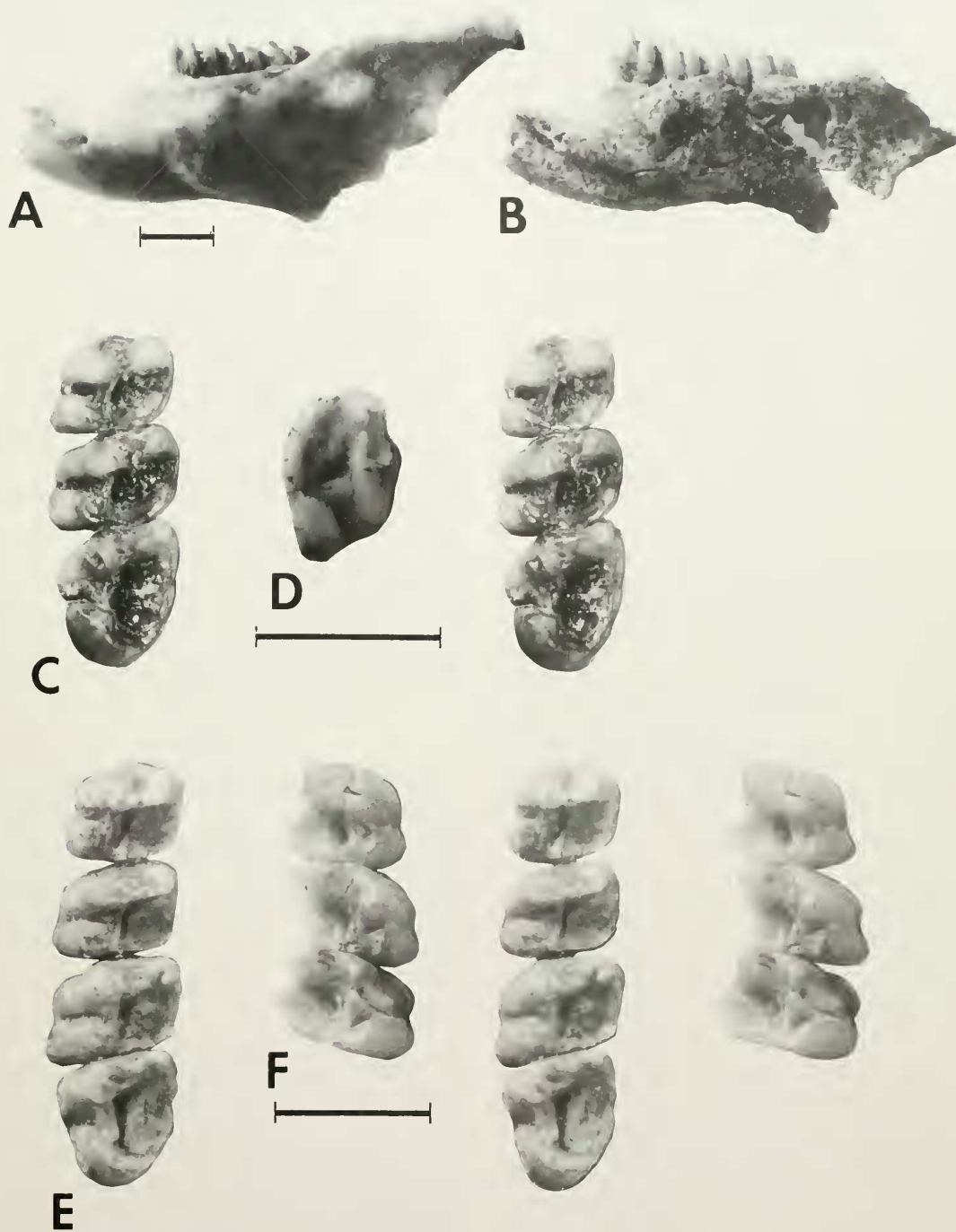


Fig. 4. Lateral view of holotype of (A) *Cynomys hibbardi* (UMMP V61648), (B) *C. sappaensis* (UNSM 11760). (C–F) Occlusal views of dentition of (C) holotype of *C. hibbardi* and (D) RM₂ referred to *C. hibbardi* (UMMP V74510), (E) holotype of *C. sappaensis*, and (F) lower dentition referred to *C. sappaensis* (UNSM 11759). All occlusal views but (D) are stereophotos. Scale bars represent 5 mm. Scale bar under (A) also applies to (B); scale bar under (F) also applies to (C) and (E).

Table 4. Measurements of lower jaws/dentition for several fossil prairie dogs.

Variable	<i>C. hibbardi</i>		<i>C. sappaensis</i>	
	UMMP V61648	UMMP V74510	UNSM 11759	UNSM 11760
ANTJW	—	—	21.10	—
MDALV	13.65	—	13.80	—
LP ₄	—	—	3.31	3.05
WTRP ₄	—	—	—	3.64
WTLP ₄	—	—	—	3.88
LM ₁	2.91	—	3.03	2.88
WM ₁	3.80	—	—	3.92
LM ₂	3.06	3.21	3.13	3.10
WM ₂	4.04	4.09	—	4.20
LM ₃	4.11	—	—	4.08
WM ₃	4.09	—	—	3.89

COMMENTS

Cynomys hibbardi resembles other prairie dogs in a number of respects—the proportions of the diastema, position of the mental foramen, development of the metalophid on M₃, and several other features. I agree with Eshelman (1975) that the species should be included within the genus *Cynomys* instead of the genus *Spermophilus*. However, it is possible that many of these prairie dog-like features evolved in parallel, and more complete material is needed in order to more fully assess the affinities of this species.

Eshelman (1975) further suggested that the species be assigned to the subgenus *Cynomys*. It resembles that subgenus in several features, but most of these similarities probably are primitive for the genus (e.g., absence of a bridge connecting the ectolophid and talonid on M₃; anteriorly deflected hypoconid on M₃; transversely narrow cheek teeth). Indeed, the species appears to be primitive with regards to the morphology of prairie dogs in most respects, and I believe it is best treated as a species with uncertain subgeneric affinities. It may lie close to the ancestry of all later taxa.

Cynomys hibbardi is clearly distinguishable from later fossil prairie dogs on a number of features, notably its lower crowned teeth and less developed metalophid on M₃. It appears to be more advanced than ?*C. vetus* in the more elongate posterior molars (see the account of that species).

The type specimen was recovered from the same horizon as UMMP V61649, a relatively complete right lower jaw with heavily worn P₄–M₃ that resembles *Cynomys hibbardi* in overall size (Eshelman, 1975). However, this specimen differs in several respects from the type, and it is not clear that it represents the same species.

Subgenus *Cynomys* Rafinesque, 1817

Figures 5A, 5C, 5E, 6A, 6C, 6E

Type Species.—As for the genus.

Geologic and Geographic Range.—Early Irvingtonian (Sappan) to Recent; restricted throughout its history to mid-continental North America.

Emended Diagnosis.—*Cynomys*, distinguished from all other prairie dogs by a large, high ridge bordering anterior cingulum of P₃; from ?*C. vetus* by more elongate M₃; from *C. hibbardi* by better developed metalophid on M₁ and M₂; and from the subgenus *Leucocrossuromys* by a strongly developed jugal triangle, less wide trigonid on P₄ (relative to the width across the talonid), absence of a bridge between the talonid and ectolophid of M₃, and the strong anterior deflection of the hypoconid on M₃.

DESCRIPTION

Skull and upper dentition.—Distinctive aspects of the skull and upper dentition are shown in Fig. 5A, C, and E and can be compared with equivalent features in *Leucocrossuromys* (Fig. 5B, D, F). Viewed dorsally, the angle between the lateral margins of the rostrum and the anterodorsal margin of the zygomatic plate is typically more abrupt than in other prairie dogs, but this character exhibits considerable variation.

The well developed jugal triangle is one of the most distinctive features of the subgenus *Cynomys*, distinguishing it from the subgenus *Leucocrossuromys* (Fig. 5A). A strong suprajugal process projects dorsad and slightly anteriad from the triangle and forms the posterior margin of a robust lateral margin to the zygomatic plate. Posteriorly, the jugal triangle tapers gradually, thus the lateral surface of the zygomatic arch remains thickened along about one-half of its length.

In posterior view, the occipital plate exhibits a domed dorsal margin which follows a more or less

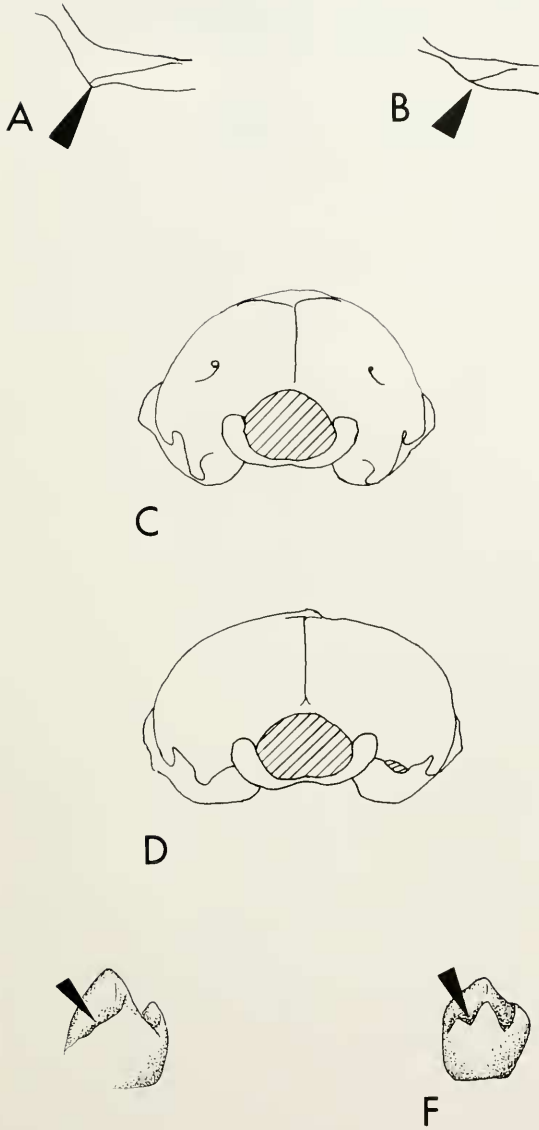


Fig. 5. Comparisons of the subgenera *Cynomys* (A, C, E) and *Leucocrossuromys* (B, D, F). (A-B) Lateral view of L jugal angle; (C-D) posterior view of occipital plate; (E-F) buccal view of the RP₃. Arrows point to subgeneric characters noted in text.

continuous arc from the level of the external auditory meatus to the dorsalmost point of the occiput (Fig. 5C), in this respect resembling most species of ground squirrels but differing from some species of *Leucocrossuromys*.

P₃ bears a well developed ridge bounding the anterior cingulum externally (Fig. 5E). This ridge

follows a more or less continuous slope from its inception near the anterolingual margin of the cingulum to its termination near the apex of the paracone. No other known prairie dog taxon, fossil or Recent, bears this conformation of the cingular ridge. Otherwise, the upper dentition of the subgenus is similar to that of *Leucocrossuromys*.

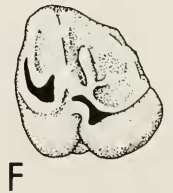
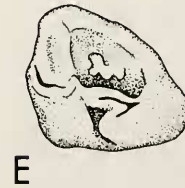
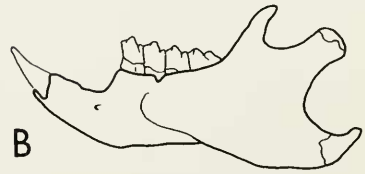
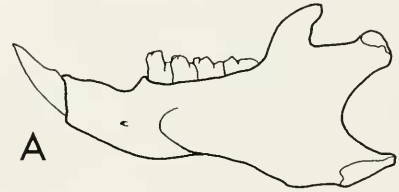


Fig. 6. Comparisons of the subgenera *Cynomys* (A, C, E) and *Leucocrossuromys* (B, D, F). (A-B) Lateral view of L lower jaw; (C-D) occlusal view of RP₄; (E-F) occlusal view of LM₃.

Lower jaw and dentition.—Aspects of the lower jaw and dentition are shown in Fig. 6 (A, C, E) and contrasted with *Leucocrossuromys* (B, D, F). On average, the portion of the lower jaw beneath the diastema is more robust than in other prairie dogs (Fig. 6A). As a result, the dorsal margin of this region, viewed laterally, tends to merge gradually with the anterior margin of the tooth row. The lower dentition is distinctive in several ways. On average, P_4 – M_3 are relatively narrow buccolingually, especially when compared to *Leucocrossuromys*. P_4 bears a buccolingually expanded trigonid, typical for prairie dogs generally, but the trigonid width is usually subequal to or less than the talonid width. This results from an enlarged, buccally expanded hypoconid (Fig. 6C).

M_1 – M_2 usually lack a developed mesolophid on the floor of the talonid, but they frequently exhibit one or more conulids, frequently oriented in a line to present an incipient mesolophid. M_3 bears several subgeneric characters, noted in the diagnosis (Fig. 6E). It usually lacks an ectostylid in the hypoflexid. The talonid platform is heavily rugose, especially along a curving ridge delimiting the anterior and buccal margins of the platform.

MORPHOMETRIC RELATIONSHIPS AMONG FOSSIL AND RECENT BLACK-TAILED PRAIRIE DOGS

I considered morphometric relationships among Recent and putative fossil black tails in order to clarify relationships and aid in making taxonomic decisions. Initial inspection of fossil material suggested the presence of three temporally successive black tails with the most recent (Late Rancholabrean) possibly divisible into two geographic morphs. The earliest, from the Early Irvingtonian (Sappan), is easy to distinguish from later members of the subgenus on qualitative features; therefore, it was not considered in this morphometric analysis. The other fossil OTUs—one from the Sheridanian and Early Rancholabrean (Illinoian and Sangamonian) and two from the Late Rancholabrean (Wisconsinan)—are similar to each other and to two extant species (*Cynomys ludovicianus*, *C. mexicanus*) in general cranial and dental morphology. These five are the initial OTUs in the following analyses. Unfortunately, the smaller of the two Late Rancholabrean morphs is only known from a few specimens recov-

ered from one locality in southeastern New Mexico. It had to be removed from statistical comparisons, although descriptive comparisons were made where possible.

Cranial analysis.—Mean values for 12 cranial variables are given for black tails in Table 5. Sample sizes for two represented fossil forms (cranial material was unavailable for the small, Wisconsinan morph) are too small to allow for meaningful statistical comparisons. However, the large Wisconsinan form resembles *Cynomys ludovicianus* in being generally larger than the Illinoian form and *C. mexicanus*.

Nine of the cranial variables were used in a PCA, and the correlations of these variables with PC1 and PC2 are given in Table 6. The pattern of correlations suggests that PC1 represents skull size, especially as reflected in variables PALP3, MXALV, PALLN, and INTOR, but with a contrast to variable PSTOR. Specimens with high scores on PC1 tend to be large, but with a relatively constricted postorbital region (PSTOR). PC2 appears to reflect a contrast between palatal width (especially as represented by PALM3) and EAML on the one hand, and MXALV and FORMH on the other. Specimens with high scores on PC2 exhibit a relatively broad palate and large external auditory meatus but a short alveolar row and low foramen magnum.

Figure 7 plots bivariate means of fossil and Recent samples on PC1 and PC2. The extant forms (*Cynomys mexicanus*, *C. ludovicianus*) are clearly distinguishable on both axes, suggesting differences in size and shape. The small sample of large Wisconsinan fossils differs from both Recent taxa, especially on PC2, but falls out closer to *C. ludovicianus* than to *C. mexicanus* on both axes. The one Illinoian specimen resembles *C. mexicanus* on PC1 but exhibits a lower score on PC2 than is typical for that species, suggesting differences in shape.

Mandibular/lower dental analysis.—Mean values for 10 mandibular/lower dental variables for black tails are shown in Table 5. Separate PCAs were performed on the anterior and posterior dental variables, and the correlations of the original variables with PC1 and PC2 are shown in Table 7. In both analyses, 78% of total variation in the original data is accounted for by PC1; this axis clearly represents general size. PC2 represents a shape axis, in both analyses reflecting a contrast between mea-

Table 5. Summary statistics for cranial and lower dental variables of two Recent and three putative fossil forms of the subgenus *Cynomys*. Sample size is given at the head of each column and is only repeated when it changes.

	<i>Cynomys</i> <i>mexicanus</i>	Illinoian black tail	<i>Cynomys</i> <i>ludovicianus</i>	Large Wisconsinan black tail	Small Wisconsinan black tail
Variable	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>
Cranial					
PALM ³	5.42 (0.42) 13	4.95 (0.28) 2	4.93 (0.39) 25	4.74 (0.65) 6	—
PALP ³	10.57 (0.56)	9.85 (0.57)	10.76 (0.52)	10.47 (0.39)	—
MXALV	15.45 (0.50)	15.72 (0.04)	16.86 (0.58)	17.65 (0.92)	—
PALLN	32.98 (1.60)	33.45 (—) 1	34.87 (1.40)	34.60 (0.54) 4	—
SKLN	53.74 (2.60)	—	56.37 (2.70)	56.45 (1.00) 3	—
INTOR	12.59 (0.97)	12.70 (—)	12.99 (0.84)	12.92 (1.10) 5	—
PSTOR	13.90 (0.81)	14.25 (—)	13.31 (1.10)	13.14 (0.78)	—
OCCPW	27.15 (0.95)	—	28.08 (0.88)	28.22 (0.66) 4	—
OCCPH	17.07 (0.75)	—	17.66 (0.81)	17.88 (0.28)	—
FORMW	8.85 (0.33)	8.75 (—)	8.84 (0.26)	8.68 (0.21)	—
FORMH	6.32 (0.60)	6.55 (—)	6.93 (0.46)	7.24 (0.61)	—
EAML	3.80 (0.30)	3.50 (—)	3.57 (0.30)	3.75 (0.09) 5	—
Mandibular/ lower dental					
MDALV	13.71 (0.30) 10	14.33 (0.54) 23	15.20 (0.54) 28	15.29 (0.57) 49	14.10 (0.40) 4
LP ₄	2.98 (0.10)	3.18 (0.16) 19	3.33 (0.16)	3.38 (0.16) 34	3.15 (0.10) 3
WTRP ₄	3.77 (0.16)	3.97 (0.31)	4.30 (0.20)	4.32 (0.28)	3.94 (0.10)
WTLP ₄	3.80 (0.20)	4.00 (0.33)	4.23 (0.23)	4.36 (0.27)	3.96 (0.23)
LM ₁	2.89 (0.17)	2.92 (0.15)	3.16 (0.14)	3.18 (0.16) 33	2.86 (0.01) 2
WM ₁	4.22 (0.12)	4.33 (0.28)	4.69 (0.21)	4.69 (0.24)	4.26 (0.04)
LM ₂	3.07 (0.12)	3.12 (0.14) 18	3.32 (0.15)	3.36 (0.16) 34	3.19 (0.10)
WM ₂	4.45 (0.11)	4.53 (0.32)	4.86 (0.19)	4.90 (0.24)	4.60 (0.05)
LM ₃	4.36 (0.19)	4.45 (0.24) 22	4.83 (0.26)	4.86 (0.27) 48	4.52 (0.13)
WM ₃	4.39 (0.14)	4.38 (0.21)	4.74 (0.18)	4.72 (0.20)	4.43 (0.07)

tures of tooth length and width (length of M₁ and M₂ had particularly high correlations with PC2 in the respective analyses). Thus, specimens with high scores on this axis tend to have relatively long teeth (especially M₁ or M₂) compared to tooth width.

Statistical comparisons were made among black tail OTUs using mean values of MDALV, PC1 derived from the anterior and posterior dentition (general measures of size), and PC2 derived from the anterior and posterior dentition (general measures of shape). Within each sample, all variables were found to be normally distributed; variances of compared samples were homogeneous except for PC1 derived from M₂–M₃.

These comparisons are displayed in Table 8; the means connected by a line are not significantly different. The large Wisconsinan form does not differ from extant *Cynomys ludovicianus* ($p > 0.1$) in any comparison. However, these two show highly significant differences ($p < 0.01$) with both the Illinoian form and extant *C. mexicanus* in all comparisons of size (MDALV, both PC1s). The Illinoian form and *C. mexicanus* are significantly different ($p < 0.05$) only in MDALV. There are no differences among groups in mean values of PC2, thus no differentiation in dental shape is evident.

Because of small sample size, the small Wisconsinan form is not included in Table 8. How-

Table 6. Correlations (loadings) of nine original cranial variables with principal component axes 1 and 2. Sample includes Recent and fossil black tails.

Variable	PC1	PC2
PALM ³	-0.15	0.81
PALP ³	0.49	0.39
MXALV	0.71	-0.52
PALLN	0.80	-0.02
INTOR	0.67	0.36
PSTOR	-0.54	0.15
FORMW	0.35	0.16
FORMH	0.13	-0.62
EAML	0.29	0.64
% total variance explained	26	23

ever, descriptive comparisons of original lower dental variables (Table 5) indicate close size resemblance to the Illinoian morph. There is also general resemblance to *Cynomys mexicanus*.

Morphometric variation in jaw proportions was examined with a bivariate plot of MDALV versus ANTJW (Fig. 8). *Cynomys mexicanus* differs from *C. ludovicianus* and the Illinoian and large Wisconsinan black tails in having a relatively low MDALV/ANTJW ratio. However, *C. mexicanus* resembles the small Wisconsinan form (marked by arrows, Fig. 8) in this character.

Taxonomic implications.—Three taxonomic judgments seem warranted. First, large Wisconsinan black tails should be referred to the extant species, *Cynomys ludovicianus*. The two forms do not differ significantly in any of the statistical comparisons. The sample of fossil skulls appears to differ from *C. ludovicianus* in aspects of shape (see the preceding cranial analysis), but two of three individuals in this sample came from essentially the same locality. The distinctive “shape” likely represents a local geographic morphotype.

Second, the Illinoian form should be distinguished taxonomically from both *Cynomys ludovicianus* and *C. mexicanus*. It differs significantly from the former in size and from the latter in mandibular proportions. Third, the small Wisconsinan form from southeastern New Mexico likely represents *C. mexicanus*. The two resemble each other in size and MDALV/ANTJW ratio.

Thus, there are four recognizable black tails: a

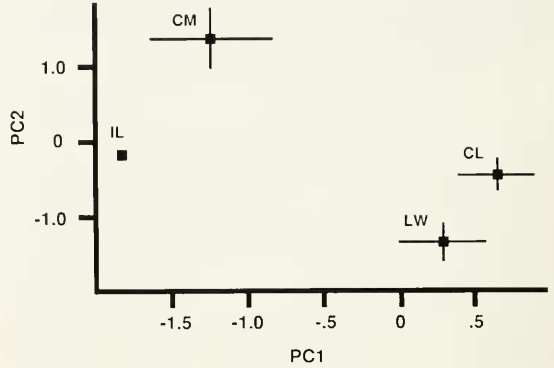


Fig. 7. Scatter plot of means of Recent and fossil black tails on PC1 and PC2 derived from analysis of cranial variables. Bars represent standard errors of means. OTU abbreviations and sample sizes are: CL, *Cynomys ludovicianus*, n = 25; CM, *C. mexicanus*, n = 13; IL, Illinoian black tail, n = 1; LW, large Wisconsin black tail, n = 3.

primitive, probable black tail from the Early Irvingtonian, and a small but advanced form from the Late Irvingtonian and Early Rancholabrean, both described herein as new species; and the two extant forms, *Cynomys ludovicianus* and *C. mexicanus*.

Cynomys (?*Cynomys*) *sappaensis*
new species

Figures 2E, 3B, 4B, 4E–F

Holotype.—UNSM 11760, left lower jaw with P₄–M₃.

Horizon and Type Locality.—Sappa Local Fauna, Early Irvingtonian (Sappan); “UNSM collection locality Hn-102 in the NW1/4 SW1/4 SE1/4 NE1/4, Sec. 11, T. 2 N., R. 20 W., Harlan County, Nebraska” (Martin and Schultz, 1985).

Referred Specimen.—UNSM 11759, right lower jaw with fragments of P₄–M₂, and UNSM 11761, left maxillary fragment with M¹–M², both from type locality.

Geologic and Geographic Range.—Known only from the type locality.

Diagnosis.—Small *Cynomys* with greater hypsodonty and higher metalophid on M₁–M₂ than *C. hibbardi*; distinguished from all later species by lesser hypsodonty and slightly less developed metalophid on M₃.

Table 7. Correlations (loadings) of original lower dental variables with principal component axes 1 and 2. Two analyses are represented, one on P_4-M_1 and another on M_2-M_3 . Samples include Recent and fossil black tails.

Variable	PC1	PC2
LP ₄	0.90	0.22
WTRP ₄	0.94	-0.20
WTLP ₄	0.90	-0.32
LM ₁	0.79	0.57
WM ₁	0.87	-0.20
% total variance explained	78	11
LM ₂	0.80	0.58
WM ₂	0.92	-0.20
LM ₃	0.92	0.06
WM ₃	0.90	-0.37
% total variance explained	78	13

Etymology.—Named after the Sappa Formation type locality, from which the holotype was recovered.

DESCRIPTION

Measurements are given in Tables 3 and 4.

Maxilla and upper dentition.—Only a fragment of the left maxilla is preserved in one referred specimen. It is shown in anterior view in Fig. 2E. The ventral portion of the zygomatic plate is preserved, and in anterior view the ventral margin appears to exhibit the deep concavity typical for *Cynomys*. The preserved portion of the palate appears to indicate posterior convergence of the tooth rows.

M_1-M_2 are triangular in occlusal outline and are much wider than long, especially M_1 (Fig. 3B). M_1 exhibits a posterior expansion of the buccal portion of the protolephid as in most later *Cynomys* and a buccally expanded anterior cingulum which extends slightly beyond the buccal margin of the paracone. Both upper teeth are less hypsodont than on later prairie dogs.

Lower jaw and dentition.—Preserved features of the lower jaw resemble *Cynomys*. In lateral view (Fig. 4B), the portion of the lower jaw beneath the diastema is robust and the mental foramen placed

Table 8. Comparisons of means among Recent and putative fossil black-tailed prairie dogs. Means connected by a line are not significantly different. Taxon abbreviations are identified in the legend of Fig. 7.

Variable	Taxon and mean			
	CM	IL	CL	LW
MDALV	13.71	14.33	15.20	15.29
	CM	IL	CL	LW
PC1: P_4-M_1	-2.98	-1.77	0.56	1.21
	LW	CM	IL	CL
PC2: P_4-M_1	-0.13	-0.09	0.04	0.11
	CM	IL	CL	LW
PC1: M_2-M_3	-2.24	-2.02	0.57	0.88
	CL	CM	LW	IL
PC2: M_2-M_3	-0.63	-0.15	0.06	0.07

anterior to the plane of the anterior root of P_4 . All cheek teeth appear to be relatively narrow on the holotype (Fig. 4E), but somewhat wider on UNSM 11759 (Fig. 4F). The trigonid on P_4 of the holotype is relatively compressed anteroposteriorly, but is more robust in this dimension on UNSM 11759. In both specimens, the protolephid is high and complete and the hypoconid is large and expanded buccally. The M_1 and M_2 of the holotype exhibit a complete, high metalophid (UNSM 11759 is worn and difficult to evaluate, but probably had a similar metalophid) and a squared off entoconid (damaged on UNSM 11759). M_3 resembles the subgenus *Cynomys* in the absence of a bridge between the talonid and ectolephid and the presence of an anteriorly deflected hypoconid. The metalophid on M_3 is complete, more developed than in *C. hibbardi*, but less developed than in later prairie dogs.

COMMENTS

There is variation in the small Sappa sample, and two forms may be present. The holotype differs from both referred specimens in the relatively lesser width of the teeth, and from UNSM 11759 in the less robust trigonid on P_4 and smaller size. However, two lines of evidence suggest that all the material represents one species. First, all specimens appear to

exhibit a similar level of hypsodonty, suggestive of a similar "stage of evolution." If the sample represents two species from significantly different time periods, one might expect that they would differ in this respect as known later forms have greater hypsodonty. Second, both of the lower jaws exhibit characteristics of black-tailed prairie dogs, and it is difficult to explain the cooccurrence of two species from the same subgenus, a pattern never documented elsewhere. There are many examples in the fossil record of two prairie dog species from the same locality, but they are always from separate subgenera. Thus, at present I believe that the within-sample variation evident in the Sappa Local Fauna probably reflects population or small-scale temporal variation in the same species.

I have tentatively placed *Cynomys sappaensis* in the subgenus *Cynomys*, based on shared features of P_4 and M_3 . However, these shared features may be primitive for prairie dogs. Available material does not preserve the derived features of P_3 and the jugal evident in other black tails, thus subgeneric placement is made tentatively. Morphologically, this species is intermediate between *C. hibbardi* and Late Irvingtonian black tails, but it is not possible with present evidence to determine if this represents an evolutionary lineage.

Cynomys (Cynomys) spenceri new species
Figure 9

Cynomys vetus: Dalquest, 1967:5.

Cynomys niobrarius: Martin, 1969:30.

Holotype.—UNSM 33798, skull preserving rostrum with right and left I_1 ; palate with left P_3 – M_3 and right P_4 – M_3 ; most of skull roof; complete right zygomatic plate with jugal; much of the occiput; and right auditory bulla.

Horizon and Type Locality.—Angus Local Fauna, Late Irvingtonian (Sheridanian); UNSM collection locality N0-101, 1 1/2 miles SW of Angus, SW 1/4, NE 1/4, Sec. 33, T4N, R6W, Nuckolls County, Nebraska (Schultz and Tanner, 1957).

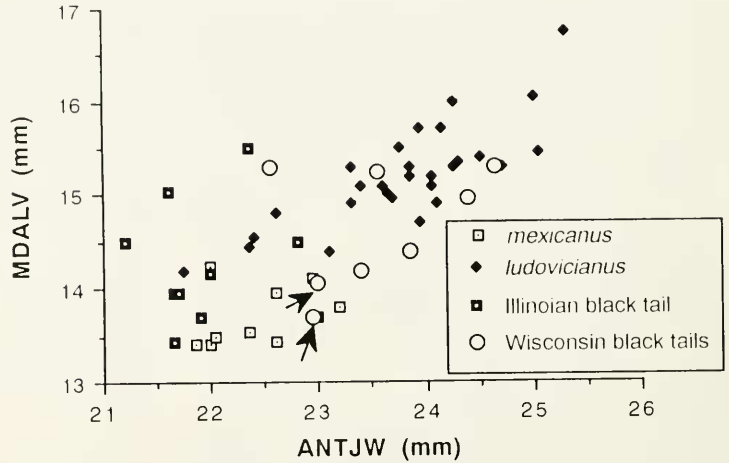


Fig. 8. Scatter plot of individual black tails on MDALV versus ANTJW. Arrows mark two Lost Valley specimens.

Referred Specimens.—See the appendix.

Geologic and Geographic Range.—Late Irvingtonian (Sheridanian) and Early Rancholabrean (Late Illinoian and Sangamonian) of the central and southern Great Plains.

Diagnosis.—Subgenus *Cynomys*; dentition averages slightly larger than *C. mexicanus* but diastema relatively shorter; averages much smaller than *C. ludovicianus*.

Etymology.—Named in honor of Dr. Lee A. Spencer, whose enthusiasm for fossil mammals and earth history sparked my interests in the same.

DESCRIPTION

Skull and upper dentition.—The holotype of *Cynomys spenceri* is shown in lateral and ventral views in Fig. 9. Upper dental measurements are provided in Table 3; average cranial measurements for the holotype and one referred specimen are provided in Table 5 (Illinoian black tail). The holotype skull exhibits two diagnostic black-tailed features—the well developed jugal angle and large, high ridge bordering the anterior cingulum of P_3 .

The Illinoian black tail plotted in Fig. 7 is the holotype of *Cynomys spenceri*. This skull resembles *C. mexicanus* in small size and broad postorbital region (low score on PC1) but differs from that taxon in exhibiting a relatively narrower palate, higher foramen magnum, and smaller external auditory meatus (low score on PC2). In these features, *C.*

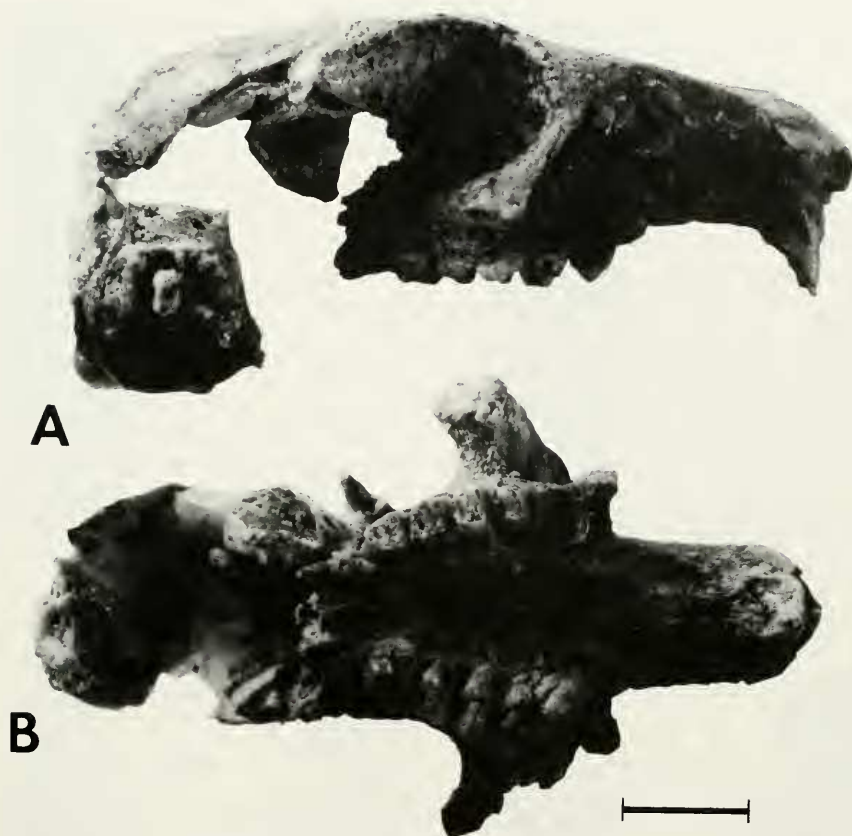


Fig. 9. Holotype of *Cynomys spenceri* (UNSM 33798) in (A) lateral, (B) ventral views. Scale bar represents 5 mm.

spenceri resembles *C. ludovicianus*. However, summary statistics for cranial variables (Table 5) indicate that *C. spenceri* (a small sample, $n = 2$) differs from *C. ludovicianus* in that the palate is relatively less constricted posteriorly (PALM³/PALP³ ratio much greater for *C. spenceri*).

Upper dentitions are known from the type and several referred specimens but do not appear to differ from *Cynomys mexicanus* and *C. ludovicianus* except in size.

Lower jaw and dentition.—Measurements of the lower jaw and dentition are given in Table 5 (Illinoian black tail). *Cynomys spenceri* averages smaller than *C. ludovicianus* in all variables and slightly larger than *C. mexicanus* in all variables except WM₃.

In most respects other than size, characteristics of the lower jaw and teeth are shared with extant black tails. However, the diastema is relatively short as in *Cynomys ludovicianus* as opposed to the long

diastema seen in *C. mexicanus*. This shortened diastema causes the relatively low values for ANTJW, and thus the higher MDALV/ANTJW ratios seen in Fig. 8. Some of the "outlying" points for *C. spenceri* on this figure may result, in part, from slight damage to the anterior end of the lower jaw, and thus to an artificially shortened diastema.

COMMENTS

Cynomys spenceri is an advanced black tail which exhibits greater morphologic similarity to *C. ludovicianus* than to *C. mexicanus*. Its temporal range probably extends from the Late Irvingtonian (Sheridanian) into the Sangamonian. Single specimens from the Sangamonian Mesa de Maya Local Fauna (UWYG 6032; Hager, 1975) and the Sangamon soil in Harlan County, Nebraska (UNSM 50778) are small, and probably referable to *C. spenceri*. However, several isolated specimens of

Early Rancholabrean (Late Illinoian) age are larger than typical of *C. spenceri*, approximating the average size of *C. ludovicianus*. Because fossil data document a continued presence of small-sized *C. spenceri* during this interval, it is possible that at least some of these specimens are intrusives from the Late Rancholabrean.

A single, isolated tooth (USNM 304236) from the Middle Irvingtonian (Cudahyan) Hall Ash Local Fauna (Eshelman and Hager, 1984) likewise seems anomalous. The specimen is probably a P_4 (the roots are not preserved so this is not certain) and morphologically resembles black tails. It resembles *Cynomys ludovicianus* in being larger than typical for *C. spenceri*. It is not clear whether this represents a large black tail preceding *C. spenceri*; chance sampling of an extreme individual from the local population (one of seven measured P_4 s from the type locality of *C. spenceri* approximates the Hall Ash specimen in size); or a Late Rancholabrean intrusive. Further work is needed to characterize this poorly known black tail from the Cudahyan interval.

Cynomys (Cynomys) ludovicianus
(Ord, 1815)
Figure 10A

Arctomys ludoviciana Ord, 1815.

Cynomys meadensis Hibbard, 1956:172.

(For a listing of synonyms in the literature of modern *Cynomys ludovicianus*, see Hollister, 1916:14, and Hall, 1981:411).

Referred Specimens.—See the appendix.

Geologic and Geographic Range.—Late Rancholabrean (Wisconsinan) of the central and southern Great Plains and across the Southwest (south of the Colorado Plateau) to southeastern Arizona; Recent of same general region and extending onto the northern Great Plains.

Emended Diagnosis.—Subgenus *Cynomys*, averaging larger than all other members of the subgenus; palate relatively more constricted posteriorly than in *C. mexicanus*.

DESCRIPTION

Skull and upper dentition.—Average cranial measurements for samples of fossil (large

Wisconsinan black tail) and Recent *Cynomys ludovicianus* are provided in Table 5. Most features of the skull and upper dentition are shared with other black tails and are described in the account of the subgenus. However, the species differs morphometrically from *C. mexicanus* in a number of respects. Fig. 7 and Table 5 suggest that *C. ludovicianus* is larger, but with a relatively more constricted postorbital region; exhibits a relatively narrower palate, especially between the M_3 s; and has a smaller external auditory meatus but higher foramen magnum (all differences contributing to low scores on PC2 in Fig. 7).

Lower jaw and dentition.—Average mandibular and lower dental measurements for fossil and Recent samples are given in Table 5, and an occlusal view of a lower dentition is shown in Fig. 10A. Again, most morphological features are shared with other black tails as described in the account of the subgenus. Like *Cynomys spenceri*, *C. ludovicianus* differs from *C. mexicanus* in its relatively shorter diastema (Fig. 8).

COMMENTS

Cynomys ludovicianus apparently arose near the beginning of the Late Rancholabrean through anagenetic change of ancestral *C. spenceri*. However, the variation within each of these chronospecies makes it difficult to precisely delimit the temporal boundary between them.

The type (UMMP 31963; Hibbard, 1956) and one referred specimen (UMMP V60532) of *Cynomys meadensis* from the Blancan Deer Park Local Fauna probably represent *C. ludovicianus*. Both specimens are high crowned and more advanced than *C. hibbardi* from the slightly younger White Rock Local Fauna, indicating that they are almost certainly intrusive. Hibbard came to this same conclusion (written communication to L. D. Martin). The type preserves only M_1 – M_2 , but UMMP V60532 preserves M_3 which exhibits a strongly deflected hypoconid, typical of black tails. The talonid platform lies adjacent to the ectolophid on this tooth, blocking the basin trench as in white tails. However, no distinct bridge is formed, and a similar conformation is sometimes seen in black tails.

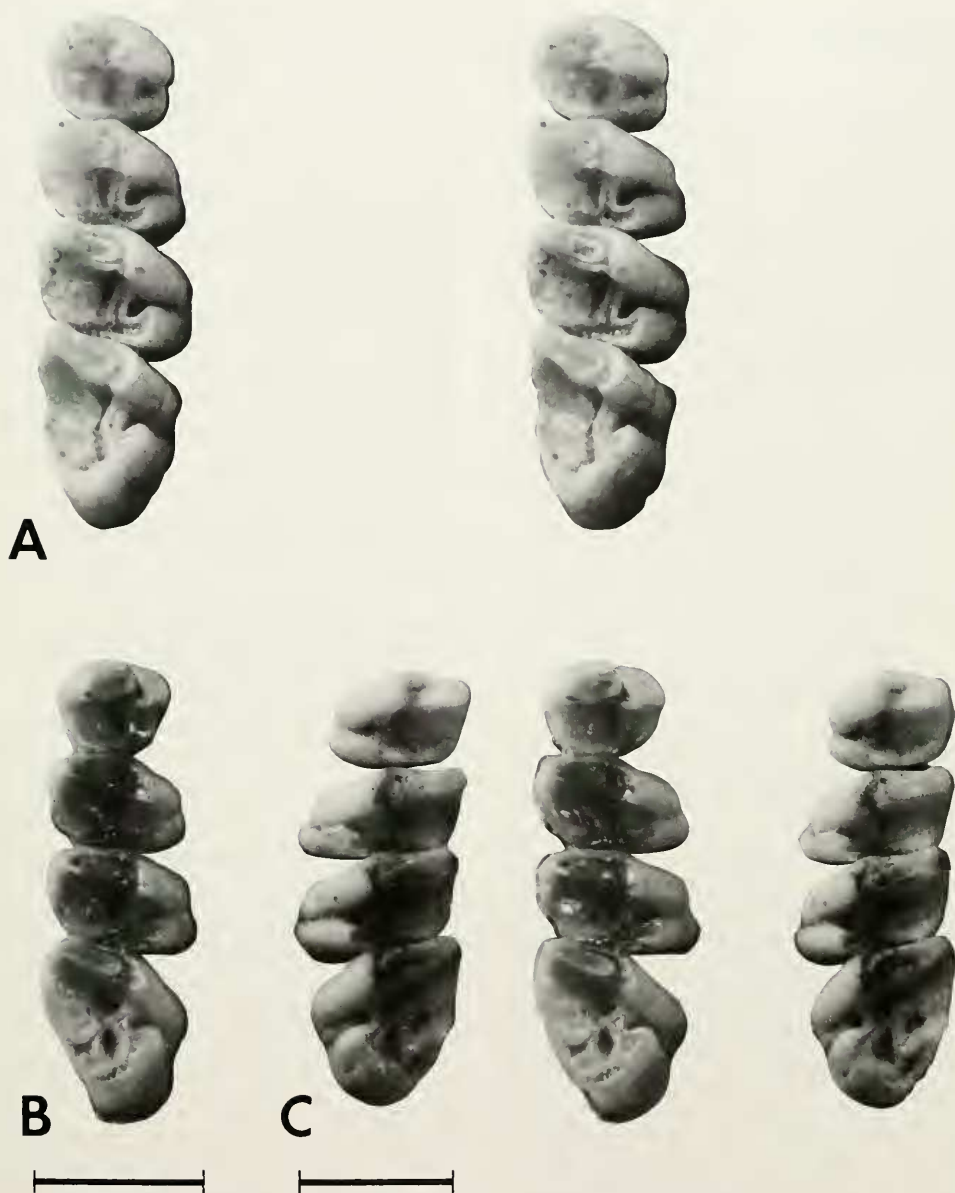


Fig. 10. Occlusal views of lower dentition, all stereophotos, for (A) *Cynomys ludovicianus* (UMMP 31759), (B) *C. gunnisoni* (TMM 41228-1691), and (C) *C. niobrarius* (KUPV 55595). Scale bars represent 5 mm; bar under (C) also applies to (A).

Hibbard (1956) diagnosed this fossil species based on the presence of a "small, round conulid, instead of a transverse mesolophid, on the lingual side of the talonid basin" of M_1 and M_2 . However, a similarly reduced "mesolophid" is encountered in other black tails. In size, both of the Deer Park

specimens approximate *Cynomys ludovicianus* more closely than *C. spenceri*, thus the assignment to the former taxon.

A single M_3 from the mid-Wisconsinan Craigmile locality, Mills County, Iowa deserves comment. The locality is dated at 23,000 yr B.P.

(Rhodes, 1984) and thus represents the mid-Wisconsinan. This specimen clearly exhibits black tail morphology but is extremely small ($LM_3 = 4.16$, $WM_3 = 4.32$; compare with Table 5), smaller than any other fossil or Recent specimen of *Cynomys ludovicianus* that I measured, approaching the size of some specimens of *C. mexicanus*. Fossils from other horizons or localities from the Great Plains thought to be of similar age (sites in Wilson County, Kansas; *Citellus* zone of southern Nebraska; Burnham Site, Wood County, Oklahoma; several sites in Denton County, Texas; see the appendix) approach average size for fossil *C. ludovicianus*, thus general size decrease during the mid-Wisconsinan is not indicated. This locality probably approximated the eastern mid-Wisconsinan range boundary for the species, and the Craigmile population may have been colonizing marginal habitat.

Cynomys (*Cynomys*)

cf. *Cynomys mexicanus* Merriam, 1892.

Referred Specimens.—See the appendix.

COMMENTS

As noted in the morphometric analysis of black tails, Recent *Cynomys mexicanus* differs from fossil and Recent *C. ludovicianus* in skull size and shape (Fig. 7), much smaller size of the lower alveolar row and dentition (Table 5), and a relatively low MDALV/ANTJW ratio (Fig. 8) resulting from the elongate diastema. *Cynomys mexicanus* has not been reported as a fossil from its present range in northeastern Mexico (Ceballos-G. and Wilson, 1985). Alvarez (1983) recently reported fossil *C. ludovicianus* from Mexico, and the possibility that these fossils are related to *C. mexicanus* needs investigation.

I tentatively refer the mid-Wisconsinan fossil black tails from Lost Valley, Eddy County, New Mexico (Harris, 1987) to this species based on overall similarity in size (much smaller than *Cynomys ludovicianus*) and on a similarly elongate diastema resulting in a low MDALV/ANTJW ratio (Fig. 8, marked by arrows). The fossils ap-

pear to be more robust in general proportions, with relatively deeper lower jaws, than is typical of *C. mexicanus*, but in this character they fall within the range of variation exhibited by Recent specimens.

If these fossils do represent *Cynomys mexicanus*, the record is of considerable interest. Southeastern New Mexico is well north of the present range of the species, indicating a more extensive range than that of today. Additionally, the record supports an origin of *C. mexicanus* prior to the mid-Wisconsinan (about 30,000 yr B.P.). Other lines of evidence support a close relationship between *C. mexicanus* and *C. ludovicianus* (Pizzimenti, 1975; McCullough and Chesser, 1987; McCullough et al., 1987). *Cynomys mexicanus* may be a Pleistocene "relict," separated from the main range of black tails by events during the Pleistocene (Hoffmann and Jones, 1970). Genetic distance has been interpreted as suggesting separation of these species about 42,000 yr B.P. (McCullough and Chesser, 1987). Thus, the Lost Valley record may represent the early history of *C. mexicanus*. This might explain the more robust lower jaws (resembling *C. ludovicianus*) than typical of *C. mexicanus*—the latter has subsequently diverged in this character from the ancestral morphotype.

Subgenus *Leucocrossuromys* Hollister, 1916
Figures 5B, 5D, 5F, 6B, 6D, 6F

Type Species.—*Cynomys gunnisoni* (Baird, 1855).

Emended Diagnosis.—*Cynomys*, distinguished from all other prairie dogs by presence of a moderately to well developed bridge connecting the ectolophid and talonid on M_3 of most specimens, reduction or loss of the strong anterior deflection of the hypoconid on M_3 , broadened trigonid and reduced hypoconid on P_4 ; further distinguished from subgenus *Cynomys* by lesser development of jugal angle and of ridge bordering anterior cingulum on P_3 .

Geologic and Geographic Range.—Probably Early Irvingtonian (Sappan) to Recent; fossil forms distributed over the northern and central Great Plains and Rocky Mountain region; Recent forms restricted to the latter.

DESCRIPTION

Skull and upper dentition.—Some distinctive aspects of the skull and upper dentition are illustrated in Fig. 5 (B, D, F) and may be compared with equivalent features in the subgenus *Cynomys* (Fig. 5A, C, E). Viewed dorsally, the angle between the lateral margins of the rostrum and the anterodorsal margin of the zygomatic plate is typically less abrupt than in the subgenus *Cynomys*, but this character is variable. Viewed laterally, the jugal lacks the prominent, downward-pointing angle (Fig. 5B) exhibited by black tails (Fig. 5A). In posterior view, the occipital plate frequently exhibits a relatively flattened dorsal margin (Fig. 5D).

The ridge bounding the anterior cingulum on P3 is typically small. In buccal view, this structure usually is terminated by a distinct notch well below the apex of the paracone (Fig. 5F). In this respect, *Leucocrossuromys* resembles advanced ground squirrels such as *Spermophilus richardsonii* but differs from the subgenus *Cynomys* which exhibits a large, well developed cingular ridge (Fig. 5E). In other respects the upper dentition is similar to that of the subgenus *Cynomys*.

Lower jaw and dentition.—Several features of the lower jaw and dentition are shown in Fig. 6 (B, D, F) and contrasted with black tails (A, C, E). Typically, the portion of the lower jaw beneath the diastema is less robust than in black tails. As a result, the dorsal margin of this region of the jaw, in lateral view, tends to drop abruptly from the anterior margin of the tooth row. The lower dentition exhibits several distinctive characters. On average, P₄–M₃ are relatively wider buccolingually across their trigonids than on black tails. P₄ is especially distinctive because the wide trigonid frequently contrasts with a narrow talonid, the latter resulting from a reduced hypoconid (Fig. 6D). This conformation of P₄ is not typical for other prairie dogs.

M₁–M₂, especially M₂, usually exhibit a moderate to large mesolophid which traverses the talonid basin buccolingually, sometimes completely dividing it into anterior and posterior portions (Dalquest, 1988). However, this structure wears rapidly and is not visible on many speci-

mens. M₃ bears several subgeneric characters (Fig. 6F) as noted in the diagnosis. The bridge between the ectolophid and talonid, and the reduction or loss of the anterior deflection of the hypoconid, are derived characters not found in other prairie dogs. The hypoflexid, between the protoconid and hypoconid, typically bears one or two ectostylids positioned externally, internally, or sometimes in both positions. These structures are only occasionally present in black tails. The talonid platform is often bounded anteriorly by a ridge coursing linguad from the point of contact between the ectolophid and talonid.

MORPHOMETRIC RELATIONSHIPS AMONG FOSSIL AND RECENT WHITE-TAILED PRAIRIE DOGS

Middle Irvingtonian (Cudahyan) and Late Rancholabrean fossils from southern Colorado and New Mexico resemble *Cynomys gunnisoni*, present in that region today, in small size and in several qualitative features. Late Irvingtonian (Sheridanian) through Late Rancholabrean fossils from the central and northern Great Plains are distinctly larger than other fossil or Recent white tails, indicating the presence of at least one extinct fossil species. However, three species of large, white tail fossils have been described, and taxonomic relationships among them need investigation. *Cynomys niobrarius*, described by Hay (1921) from a damaged, somewhat distorted skull (AMNH 2715), was recovered from Pleistocene beds in northwestern Nebraska. The fossil was collected from the vicinity of the type section for the Sheridanian (Late Irvingtonian), and the fossil may be of equivalent age; however, this is not certain. *Cynomys spispiza*, described by Green (1960) from a partial lower jaw with P₄–M₃ (SDSM 57100), was recovered from Late Rancholabrean deposits in southcentral South Dakota. Because of the geographic proximity of type localities, the two named forms probably do not represent contemporary species. However, they might represent separate chronospecies. *Cynomys churcheri* was described from a large sample of cranial and post cranial fossils (the type, PMA P85.9.12, includes most of an entire skeleton) from the northwestern Plains of southern Alberta (Burns and McGillivray, 1989). The fossil sample is Late Rancholabrean

Table 9. Summary statistics for cranial variables of three Recent and two putative fossil forms of the subgenus *Leucocrossuromys*. Sample size is given at the head of each column and is only repeated when it changes. Names of fossil OTUs correspond to putative taxa recognised in previous studies.

	<i>Cynomys gunnisoni</i>			<i>Cynomys parvidens</i>			<i>Cynomys leucurus</i>			<i>Cynomys churcheri</i>			<i>Cynomys niobrarius/spispiza</i>		
Variable	\bar{x} (sd) <i>n</i>			\bar{x} (sd) <i>n</i>			\bar{x} (sd) <i>n</i>			\bar{x} (sd) <i>n</i>			\bar{x} (sd) <i>n</i>		
PALM ³	5.45	(0.36)	11	5.51	(0.33)	5	5.47	(0.35)	15	5.06	(0.39)	15	5.17	(0.54)	9
PALP ³	9.78	(0.51)		9.67	(0.87)		9.65	(0.81)		10.90	(0.32)	14	10.41	(0.56)	7
MXALV	15.03	(0.32)		15.35	(0.74)		15.67	(0.68)		16.41	(0.34)	15	16.28	(0.81)	9
PALLN	32.53	(0.82)		33.03	(1.10)		33.66	(0.97)	14	36.00	(0.88)	13	34.62	(1.60)	5
SKLN	52.34	(1.70)		53.06	(2.20)		54.46	(1.70)		57.63	(1.40)	12	56.03	(2.50)	3
INTOR	11.65	(0.67)		12.60	(1.30)		12.32	(0.54)		12.84	(0.60)	13	12.52	(0.68)	7
PSTOR	13.84	(0.91)		14.53	(0.42)		13.62	(0.72)	15	13.30	(0.77)	12	12.53	(0.99)	6
OCCPW	27.17	(0.55)		28.37	(1.20)		28.08	(0.80)	14	29.46	(0.74)	9	28.43	(1.50)	5
OCCPH	16.37	(0.55)		16.08	(0.58)		16.75	(0.60)	15	17.41	(0.82)	11	16.91	(0.54)	
FORMW	8.05	(0.32)		8.60	(0.16)		8.73	(0.28)		8.86	(0.53)		8.27	(0.32)	3
FORMH	6.20	(0.60)		5.91	(0.38)		7.17	(0.34)		6.53	(0.40)		6.55	(0.61)	
EAML	3.49	(0.28)	10	3.56	(0.51)		3.96	(0.38)		3.83	(0.40)	7	3.79	(0.37)	5

(22,000 to 33,000 yr B.P.) and might represent a geographically distinct contemporary of *C. spispiza*.

To assess taxonomic relationships, I investigated morphometric relationships among Recent species (*Cynomys gunnisoni*, *C. leucurus*, *C. parvidens*) and the following putative fossil taxa: *C. cf. gunnisoni* (small white tails from the southern Rockies), *C. niobrarius* (herein including large Sheridanian and Early Rancholabrean white tails), *C. spispiza* (large Late Rancholabrean white tails south and east of southern Alberta), and *C. churcheri* (large Late Rancholabrean white tails from southern Alberta).

Cranial analysis.—Mean values for 12 cranial variables are given in Table 9. *Cynomys niobrarius* and *C. spispiza* are combined because of small sample sizes, and fossil *C. cf. gunnisoni* is not included because appropriate material was unavailable. Five cranial variables are used in a PCA, and the correlations of these variables with PC1 and PC2 are given in Table 10. The pattern of correlations suggests that PC1 primarily represents skull size as reflected by variables PALP³, MXALV, and INTOR, and secondarily reflects a contrast between these variables and PALM³ and PSTOR. Specimens with high scores on PC1 tend to be large, but with relatively constricted posterior palates (PALM³) and postorbital regions (PSTOR). PC2 reflects width of the skull roof (INTOR, PSTOR) and of the posterior palate (PALM³).

Figure 11A plots bivariate means of fossil and Recent skulls on PC1 and PC2. Statistical comparisons of mean values of PC1 and PC2 are given in Table 11. There are no differences among Recent or between represented fossil OTUs in PC1 ($p > .1$ in all cases), but both fossil samples differ significantly ($p < .01$) from the three Recent forms in this variable. High values of PC1 for fossil forms reflect large size contrasting with relatively narrow posterior palates and postorbital regions, a pattern also detectable from inspection of Table 9. There are no significant differences among white tails on PC2, but the difference between *Cynomys niobrarius/spispiza* and *C. parvidens* approached statistical significance ($.05 < p < .1$).

Mandibular/lower dental analysis.—Mean values for 10 mandibular/lower dental variables are shown in Table 12. Seven variables (measurements of P₄–M₂) were used in a PCA, and the correlations of original variables with PC1 and PC2 are given in Table 10. Of the total variation in the original set of seven variables, 78% was accounted for by PC1, and this clearly represents general size. PC2 represents a shape axis, reflecting contrast between two measures of length (LM₁, LM₂; LP₄ was not highly

Table 10. Correlations (loadings) of five original cranial and seven original lower dental variables with PC1 and PC2. Two analyses are represented, one on cranial and the other on lower dental variables. Samples include Recent and fossil white tails.

Variable	PC1	PC2
PALM ³	-0.39	0.76
PALP ³	0.81	0.26
MXALV	0.73	-0.03
INTOR	0.63	0.68
PSTOR	-0.49	0.64
% total variance explained	39	30
LP ₄	0.90	0.17
WTRP ₄	0.91	-0.33
WTLP ₄	0.87	-0.29
LM ₁	0.84	0.49
WM ₁	0.90	-0.23
LM ₂	0.84	0.50
WM ₂	0.90	-0.25
% total variance explained	78	12

correlated with this axis) and all four measures of width. Specimens with high scores on PC2 tend to have relatively long teeth (especially M₁–M₂) compared to tooth width.

Figure 11B plots bivariate means of fossil and Recent samples on PC1 and PC2. Statistical comparisons of mean values for MDALV, PC1, and PC2 are given in Table 11. Variation among three Recent white tails is not significant in any comparison. This reflects morphologic similarity among Recent species, but with larger sample sizes some significant differences probably would be detected. Fossils referred to *Cynomys gunnisoni* do not differ from extant *C. gunnisoni* in any comparison. The three large fossil forms differ significantly ($p < .01$) from all Recent samples and fossil *C. cf. gunnisoni* in comparisons of size (MDALV, PC1). There are no differences among the three, large fossil forms in comparisons of size ($p > .1$). However, *C. churcheri* is significantly ($p < .01$) different from *C. niobrarius* and *C. spispiza* in comparisons of shape (PC2). No significant differences are evident between *C. niobrarius* and *C. spispiza*.

Taxonomic implications.—Three taxonomic judgments seem warranted. First, fossils referred to *Cynomys gunnisoni* do represent that species. Second, large fossils from the northern and central Plains are distinct from all extant white tails, and this

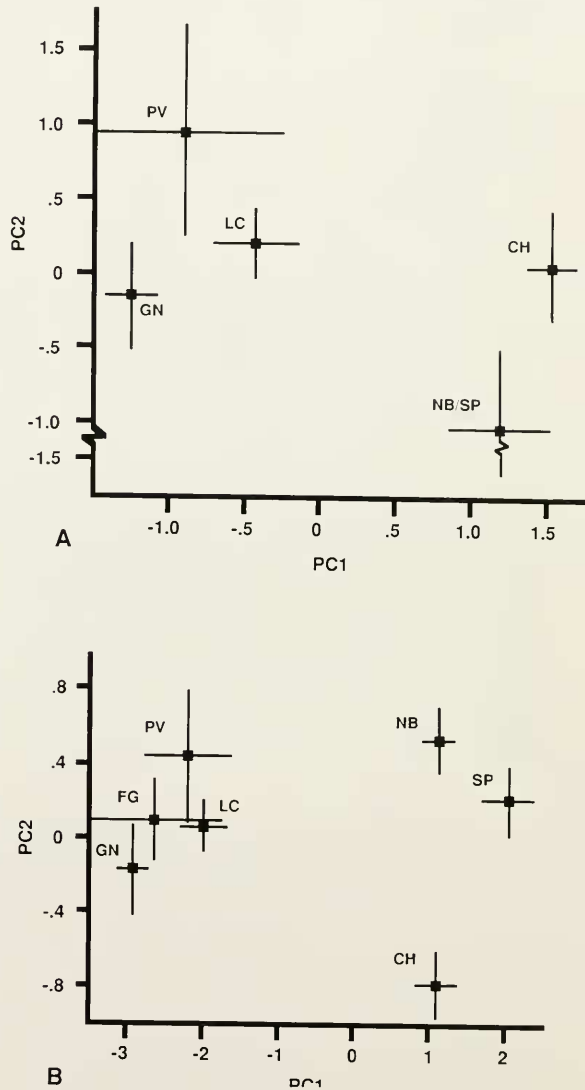


Fig. 11. Scatter plots of means of Recent and fossil white tail OTUs on PC1 and PC2. (A) PCs derived from analysis of five cranial variables; (B) PCs derived from analysis of seven lower dental variables. Bars represent standard errors of means. OTU abbreviations are identified in Table 11. Sample sizes for: (A) CH, $n = 11$; GN, $n = 11$; LC, $n = 14$; NB/SP, $n = 6$; PV, $n = 6$. (B) CH, $n = 21$; FG, $n = 6$; GN, $n = 15$; LC, $n = 19$; NB, $n = 24$; PV, $n = 6$; SP, $n = 21$.

Table 11. Comparisons of means among Recent and putative fossil white-tailed prairie dogs. Means connected by a line are not statistically different. OTU abbreviations used are: CH, *C. churcheri*; FG, fossils referred to *C. gunnisoni*; FW, fossil white tails (combined *C. niobrarius* and *C. spispiza*); GN, *C. gunnisoni*; LC, *C. leucurus*; NB, *C. niobrarius*; PV, *C. parvidens*; SP, *C. spispiza*. Names of fossil OTUs correspond to putative taxa recognized in previous studies.

Variable	Taxon and mean				
	GN	PV	LC	FW	CH
PC1: Cranial	-1.30	-0.89	-0.42	1.20	1.50
PC2: Cranial	FW	GN	CH	LC	PV
	-1.00	-0.15	0.06	0.18	0.94
MDALV	FG	GN	PV	LC	CH
	13.30	13.50	13.70	13.90	14.60
PC1: P ₄ -M ₂	NB	SP	LC	CH	GN
	14.80	14.90	13.90	14.60	13.50
PC2: P ₄ -M ₂	GN	FG	PV	LC	CH
	-2.90	-2.60	-2.20	-2.00	1.10
PC1: P ₄ -M ₂	NB	SP	LC	CH	GN
	1.20	2.00	-2.00	1.10	-2.90
PC2: P ₄ -M ₂	CH	GN	FG	LC	SP
	-0.78	-0.18	0.11	0.11	0.29

should be recognized taxonomically. Third, the similarity among all three samples of large fossil white tails probably indicates that they are conspecific (*C. niobrarius*). Shape differences between the northern *C. churcheri* and southern *C. niobrarius* and *C. spispiza* appear to be meaningful, but can be interpreted as geographic variation within a single, widespread species, perhaps representing subspecific differentiation.

Cynomys (Leucocrossuromys) gunnisoni
(Baird, 1855)
Figure 10B

Spermophilus gunnisoni Baird, 1855.
(For a listing of synonyms in the literature of modern *Cynomys gunnisoni*, see Hollister, 1916:29 and Hall, 1981:414–415).

Referred Specimens.—See the appendix.

Geologic and Geographic Range.—?Middle Irvingtonian (Cudahyan) to Recent of the southern Rocky Mountains and adjacent highlands.

Emended Diagnosis.—Subgenus *Leucocrossuromys*, averaging smaller than other white tails; distinguished by less consistent development of bridge connecting ectolophid and talonid on M₃ and lesser reduction of the anterior deflection of hypoconid on M₃.

DESCRIPTION

Skull and upper dentition.—Average cranial measurements for a sample of Recent *Cynomys gunnisoni* are given in Table 9. Most features of the skull and upper dentition are common to *Leucocrossuromys*. However, skulls of *C. gunnisoni* differ in three respects. First, the jugal angle, although less developed than in black tails, is often more developed than in other white tails. Second, the dorsal margin of the occiput usually is less flattened than in other white tails (Fig. 5D), although it is not typically as domed as in black tails (Fig. 5C). Third, the posterodorsal margins of the premaxillae frequently extend posteriorly beyond the nasals on the skull roof, more so than is typical for other white tails. The upper dentition is characteristic of white tails.

Lower jaw and dentition.—Average mandibular and lower dental measurements for fossil and Recent samples are given in Table 12. Most morphological features are shared with other white tails as described in the account of the subgenus. However, *Cynomys gunnisoni* exhibits less consistent development of the bridge between the ectolophid and talonid and lesser reduction of the anterior deflection of the hypoconid on M₃. The latter feature can be seen in Fig. 10B, in contrast to Fig. 10C. Some specimens approach the state exhibited by black tails.

Table 12. Summary statistics for mandibular and lower dental variables of three Recent and four putative fossil forms of the subgenus *Leucocrossomys*. Sample size is given at the head of each column and is only repeated when it changes. Names of fossil OTUs correspond to putative taxa recognized in previous studies.

Variable	Fossil							
	<i>Cynomys cf. gunnisoni</i>	<i>Cynomys gunnisoni</i>	<i>Cynomys parvidens</i>	<i>Cynomys leucurus</i>	<i>Cynomys niobrarius</i>	<i>Cynomys churcherii</i>	<i>Cynomys spispiza</i>	
	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	\bar{x} (sd) <i>n</i>	
MDALV	13.25 (0.58) 10	13.48 (0.40) 16	13.67 (0.40) 6	13.94 (0.49) 19	14.82 (0.36) 33	14.56 (0.37) 21	14.91 (0.69) 24	
LP ₄	2.79 (0.09) 9	2.79 (0.09) 15	2.83 (0.12)	2.92 (0.13)	3.20 (0.11) 36	3.08 (0.11)	3.22 (0.15) 25	
WTRP ₄	3.91 (0.22)	4.00 (0.17)	3.96 (0.24)	4.03 (0.21)	4.46 (0.20)	4.60 (0.19)	4.54 (0.26)	
WTLP ₄	3.70 (0.21)	3.71 (0.20)	3.67 (0.23)	3.75 (0.27)	4.15 (0.21)	4.11 (0.28)	4.22 (0.27)	
LM ₁	2.76 (0.08) 8	2.76 (0.14)	2.85 (0.14)	2.83 (0.11)	3.10 (0.14) 34	2.98 (0.14)	3.17 (0.16) 28	
WM ₁	4.35 (0.09)	4.40 (0.09)	4.52 (0.25)	4.49 (0.20)	4.90 (0.18)	5.18 (0.22)	5.09 (0.31)	
LM ₂	2.95 (0.14) 6	2.96 (0.12)	3.12 (0.12)	3.07 (0.14)	3.28 (0.16) 35	3.19 (0.12)	3.38 (0.19)	
WM ₂	4.54 (0.15)	4.67 (0.11)	4.82 (0.27)	4.90 (0.20)	5.13 (0.20)	5.39 (0.21)	5.35 (0.31)	
LM ₃	4.37 (0.18) 13	4.59 (0.11)	4.54 (0.18)	4.68 (0.23)	4.99 (0.16) 33	4.90 (0.20)	4.99 (0.23) 27	
WM ₃	4.44 (0.12)	4.58 (0.12)	4.87 (0.14)	4.91 (0.23)	5.02 (0.25)	5.18 (0.20)	5.19 (0.27)	

COMMENTS

Cynomys gunnisoni clearly is a member of the subgenus *Leucocrossuromys* as indicated by several shared, derived characters. However, the species differs in the degree to which some characters are developed. In several cases (shape of the occiput, states of the bridge and hypoconid on M_3), *C. gunnisoni* probably is primitive for white tails. This is consistent with previous interpretations that the species is primitive in aspects of its biology (Nadler et al., 1971; Pizzimenti, 1975).

Fossils referred to *Cynomys gunnisoni* resemble Recent specimens in most respects, indicating little change in this lineage since the Pleistocene. However, fossils appear to differ in the relatively smaller (especially shorter) M_3 (Table 12). The meaning of this difference is not clear, but it does not in itself warrant the erection of a new taxon.

The record of *Cynomys gunnisoni* from the Hansen Bluff Local Fauna, Alamosa County, Colorado (Rogers et al., 1985), suggests a history back to the Cudahyan. The Hansen Bluff fossils are indistinguishable from Late Rancholabrean *C. gunnisoni*, and possible intrusiveness must be considered. However, there was no field evidence that the prairie dog fossils were out of context (Rogers, pers. comm.).

Cynomys (Leucocrossuromys) niobrarius

Hay, 1921

Figure 10C

Cynomys niobrarius Hay, 1921:615.*Cynomys spispiza* Green, 1960:545.*Cynomys* cf. *leucurus*: McDonald and Anderson, 1975:25.*Cynomys churcherii* Burns and McGillivray, 1989:2637.

Holotype.—AMNH 2715, a partial, somewhat distorted skull preserving the palate with some teeth.

Horizon and Type Locality.—Late Pleistocene, possibly Sheridanian; locality given only as "Niobrara River, near Grayson, Nebraska" (Hay, 1921).

Referred Specimens.—See the appendix.

Geologic and Geographic Range.—Late Irvingtonian (Sheridanian) to Late Rancholabrean of the northern and central Great Plains and adjacent portions of the central Rocky Mountains.

Emended Diagnosis.—Subgenus *Leucocrossuromys*, much larger than all other members of subgenus; like *Cynomys leucurus* and *C. parvidens*, consistently exhibits well developed bridge between ectolophid and talonid of M_3 and extreme reduction or loss of anterior deflection of hypoconid on M_3 .

DESCRIPTION

Skull and upper dentition.—Average cranial measurements for two samples of *Cynomys niobrarius* are given in Table 9 (*C. niobrarius*/*C. spispiza*, *C. churcherii*). The most distinctive feature of this taxon is its large size. In addition, its skull differs from Recent species in shape. Based on the interpretation of PC1 presented previously, *C. niobrarius* appears to have a relatively narrower posterior palate and postorbital region, a pattern evident with inspection of Table 9.

Most qualitative features of the skull and upper dentition are shared with other white tails and are described in the account of the subgenus. *Cynomys niobrarius* resembles *C. leucurus* and *C. parvidens*, but differs from *C. gunnisoni* in that it typically exhibits a reduced jugal triangle and a more flattened dorsal profile of the occipital plate.

Lower jaw and dentition.—Average mandibular and lower dental measurements for three samples of *Cynomys niobrarius* are provided in Table 12 (*C. niobrarius*, *C. spispiza*, *C. churcherii*). Other than size, *C. niobrarius* differs in few respects from *C. leucurus* and *C. parvidens*. However, it differs from *C. gunnisoni* in the more developed bridge between the ectolophid and talonid on M_3 , and in the greater reduction of the anterior deflection of the hypoconid on M_3 . The latter feature can be seen in Fig. 10C.

COMMENTS

All three fossil species synonymized here clearly are members of the subgenus *Leucocrossuromys*. Hay (1921) did not formally assign *Cynomys niobrarius* to either subgenus, but he pointed out several similarities between the type and *C. leucurus*. However, the characters he used were not diagnostic. Dalquest (1967) considered this species to be related to the subgenus *Cynomys* but presented no supporting evidence. Fortunately, the unerupted P_3 can be seen through the opening left by the dP_3 , and

the conformation of the ridge bounding the anterior cingulum is that of *Leucocrossuromys*. Likewise, Green (1960) did not formally assign *C. spispiza* to either subgenus but suggested that it might be closer to *C. leucurus* than to *C. ludovicianus*. All preserved features of the lower dentition support white tail affinities. This taxon initially was thought to be from the Tertiary (Green, 1960) but subsequently was found to be Late Pleistocene in age (Green, 1963). *Cynomys churcherii* was assigned to *Leucocrossuromys* in the original description (Burns and McGillivray, 1989), an assignment abundantly supported by cranial and dental evidence.

I decided to synonymize these three fossil forms at the species level based on two lines of evidence. First, the types and referred fossil samples resemble each other in general size and morphology and appear to be within the range of variation expected of a single species. Second, all three forms occupied the same general geographic region during the Late Pleistocene, namely, the northern Great Plains.

The one example of significant variation within *Cynomys niobrarius* is in dental shape as reflected in PC2 derived from the analysis of P_4-M_2 (Table 9). *Cynomys churcherii* has significantly wider teeth relative to tooth length (large, negative values on PC2) than the southern *C. niobrarius* and *C. spispiza*. Thus, the northern sample appears to represent a distinct geographic form, divergent from southern populations of *C. niobrarius*. I have followed standard taxonomic practice and recognize the northern and southern morphs as separate subspecies.

Cynomys niobrarius niobrarius Hay, 1921

Cynomys niobrarius Hay, 1921:615.

Cynomys spispiza Green, 1960:545.

Cynomys cf. *leucurus*: McDonald and Anderson, 1975:25.

Holotype.—As for species.

Horizon and Type Locality.—As for species.

Referred Specimens.—See the appendix.

Geologic and Geographic Range.—Known from the Sheridanian through Late Rancholabrean of the central and northern Great Plains and adjacent areas approximately to the present northern boundary of the United States.

Emended Diagnosis.—*Cynomys niobrarius*, differing from *C. niobrarius churcherii* in relatively narrower lower cheek teeth.

Cynomys niobrarius churcherii Burns and McGillivray, 1989

Cynomys churcherii Burns and McGillivray, 1989:2637.

Holotype.—PMA P.85.9.12, a virtually complete skeleton with skull, lower jaws, and complete dentition.

Horizon and Type Locality.—From burrows, dated at 22,000 to 33,000 yr B.P., intruding the Miocene Hand Hills Formation; "Winter site gravel pit, in the Hand Hills, 28 km NE of Drumheller, Municipal District of Starland, Alberta" (Burns and McGillivray, 1989).

Referred Specimens.—See the appendix.

Geographic and Geologic Range.—Known only from the mid-Wisconsinan of the Hand and Wintering Hills, southern Alberta.

Emended Diagnosis.—*Cynomys niobrarius*, differing from *C. niobrarius niobrarius* in the relatively wider lower cheek teeth.

COMMENTS

The position of the boundary between *Cynomys niobrarius churcherii* and *C. niobrarius niobrarius* is not clearly defined. *Cynomys niobrarius* has been recovered from deposits of Sheridanian, Early Rancholabrean (Sangamonian), and Late Rancholabrean age in the Medicine Hat sequence of southeastern Alberta (Stalker and Churcher, 1970). Unfortunately, only two of these specimens are sufficiently complete for use in the PCA of P_4-M_2 . These resemble the southern form more than *C. niobrarius churcherii* in tooth shape, but the sample is too small to allow for statistical comparisons.

Cynomys sp.

I was unable to study reported prairie dog fossils from three important localities. These fossils either could not be found or were under study by other investigators.

Stalker and Churcher (1970) listed *Cynomys* cf. *meadensis* as part of the Wellsch Valley Local Fauna

from southern Saskatchewan. Specific identification almost certainly was based on the age of these fossils—*C. meadensis* once was thought to be very old (Hibbard, 1956)—and the Wellsch Valley specimens probably have nothing to do with *C. meadensis* (= *C. ludovicianus*, as synonymized in this paper). However, if these fossils represent the genus *Cynomys* (which is not certain), they would be of great interest because of the age (probably Sappan, possibly younger; Churcher, pers. comm.) and geographic position of the locality.

Semken (1966) reported *Cynomys* cf. *gunnisoni* from the Kentuck Local Fauna, McPherson County, Kansas, a fauna generally thought to be Sappan in age. He reported the presence of a bridge connecting the ectolophid and talonid on M_3 , thus these fossils probably represent an early member of the subgenus *Leucocrossuromys*. The record is of considerable interest because of the age of the fauna.

Barnosky and Rasmussen (1988) listed two unnamed species of *Cynomys* from Porcupine Cave, Park County, Colorado. The site is significant because of its age (near 400 ky B.P.) and location (high elevation—2900 m—in the central Rocky Mountains). These fossils may shed light on regional prairie dog biogeography and evolution.

In addition to these faunas, three specimens that I have examined deserve comment. A right lower jaw with P_4 – M_3 (FHSU VP-6931) recovered from the Williams Farm locality, Rice County, Kansas, is thought to be “Illinoian” in age (Holman, 1984). The teeth are somewhat worn, but the shape of P_4 and presence of a bridge connecting the ectolophid and

talonid on M_3 appear to support white tail affinities. The fossil, however, exhibits greater anterior deflection of the hypoconid on M_3 and smaller overall size than typical of *Cynomys niobrarius*. The conformation of the M_3 hypoconid resembles *C. gunnisoni*, but the fossil is larger than typical of that species. This fossil may simply reflect normal variability in Illinoian *C. niobrarius*. Alternatively, it may represent a somewhat earlier stage in the evolution of white tails on the Great Plains, in which case the fauna probably predates the Illinoian.

A left lower jaw with P_4 – M_3 (FHSU VP-7065) was recovered from Harper 21C, McPherson County, Kansas, a locality of uncertain but possibly Early Rancholabrean age. In contrast to the Williams Farm specimen, this fossil exhibits black tail characteristics of the P_4 and the hypoconid on M_3 , suggesting affinities with the subgenus *Cynomys*. However, the M_3 bridge is extremely well developed, more so than in any other black tail that I have examined. Thus, the taxonomic placement of this specimen remains uncertain.

A left lower jaw with P_4 – M_3 (UWYG 3392) was recovered from Chimney Rock Animal Trap, a mixed Late Pleistocene/Holocene locality in Larimer County, northcentral Colorado (Hager, 1972). The specimen clearly represents a white tail, but is smaller than any specimen of *Cynomys niobrarius* I have examined (MDALV, 13.6; compare with Table 12). However, UWYG 3392 resembles all three Recent white tails. Most likely, this fossil represents *C. leucurus*, present locally today. It is almost certainly Holocene in age.

PHYLOGENETIC RELATIONSHIPS

Hypotheses of relationships among Recent and fossil species of *Cynomys* are given in Fig. 12. Analysis of 19 characters (Table 13) using PAUP resulted in three equally parsimonious trees, shown in Figs. 12A–C. Each of these trees requires 27 steps and has a consistency index of 0.963.

These three phylogenetic hypotheses are very similar, differing only in the positions of ?*Cynomys vetus* and *C. hibbardi* relative to each other. There are many missing characters for these two species (Table 13), making it difficult to resolve their relationships. Two trichotomies are evident in all trees (*C. spenceri*–*ludovicianus*–*mexicanus* and *C. niobrarius*–*leucurus*–*parvidens*), reflecting identical sets of character states among species in each triad (Table 13).

An alternative phylogenetic hypothesis, which I

currently favor, combines character and stratigraphic data (Fig. 12D). *Cynomys spenceri* and *C. niobrarius* are considered ancestral in their respective lineages based on stratigraphic occurrence and appropriate ancestral morphology. *Cynomys sapphaensis* is considered ancestral to later black tails, not the sister group of all advanced black tails and white tails as suggested by Figs. 12A–C. This relationship is suggested by the probable presence of a white tail in deposits of similar age at the Kentuck locality (Semken, 1966), suggesting that the split between subgenera had already occurred. Not surprisingly, ?*C. vetus* and *C. hibbardi*, which are least derived morphologically, are also the oldest species of prairie dogs currently known. Available evidence suggests that ?*C. vetus* is somewhat more primitive than *C. hibbardi*.

The relationships among Recent species suggested in Fig. 12 are consistent with other lines of evidence. Close relationships have been suggested between *Cynomys leucurus* and *C. parvidens* based on karyotype and other features (Pizzimenti and

Nadler, 1972), and between *C. mexicanus* and *C. ludovicianus* based on genic data (McCullough and Chesser, 1987). The monophyletic relationship of *C. gunnisoni* to other white tails is consistent with immunologic evidence (McCullough et al., 1987).

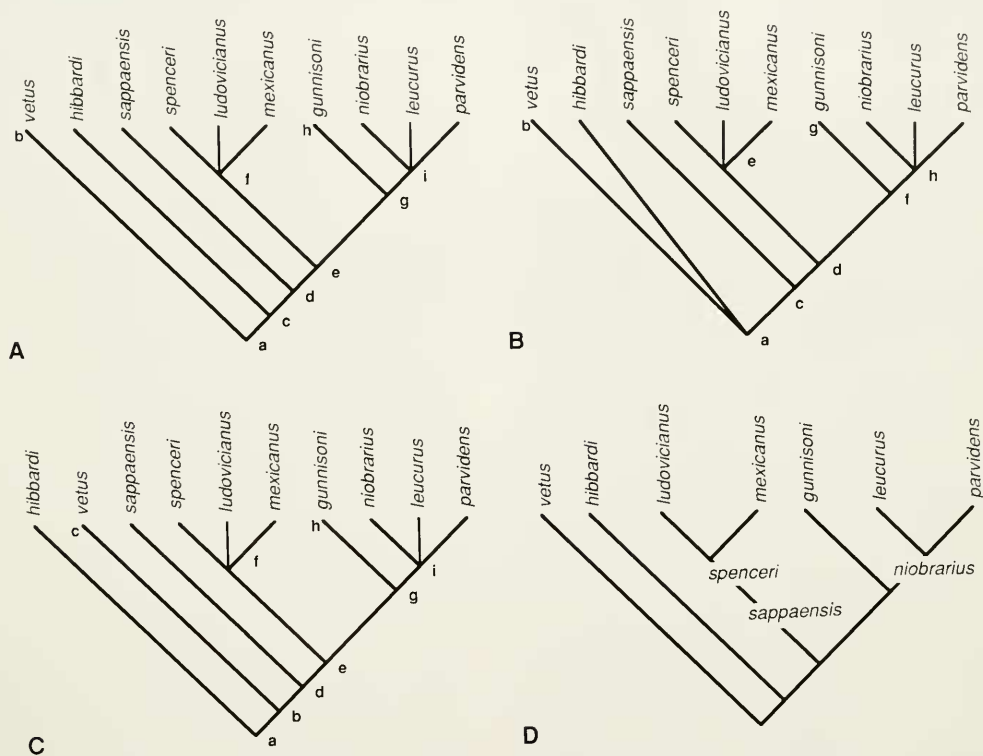


Fig. 12. (A-C) Hypotheses of relationships among fossil and Recent species of *Cynomys* obtained by an analysis of cranial, mandibular, and dental characters (see Table 13 and text). Derived characters are given below for each tree; if no state is indicated, the transition is from state 0 to 1. (A) **a**: 2(1), 5, 7, 11, 13, 14(1), 15, 17(1); **b**: 12(0); **c**: 3, 6, 9; **d**: 8(1), 17(2); **e**: 8(2); **f**: 2(2), 10; **g**: 4(1), 14(2), 16, 18(1), 19(1); **h**: 1; **i**: 2(0), 4(2), 18(2), 19(2). (B) **a-b**: same as tree A, nodes **a-b**; **c**: 3, 6, 8(1), 9, 17(2); **d-h**: same as tree A, corresponding nodes **e-i**. (C) **a**: same as tree A, node **a**; **b**: 8(1), 17(2); **c**: 12(0); **d**: 3, 6, 9; **e-i**: same as tree A, nodes **e-i**. (D) Hypothesis which incorporates stratigraphic position of taxa.

SUMMARY

Eight species of prairie dogs, genus *Cynomys*, are recognized in the fossil record. *?Cynomys vetus* and *C. hibbardi* are early (Late Blancan and/or Early Irvingtonian), primitive forms of uncertain subgenus. *Cynomys sappaensis*, described herein from the Early Irvingtonian of Nebraska, probably is a primitive member of the subgenus *Cynomys*. Another new species, *C. spenceri*, is known from the Late Irvingtonian and Early Rancholabrean of the Great Plains. It is a small but advanced member of the subgenus *Cynomys* probably ancestral to *C. ludovicianus*, known from the Late Rancholabrean

and Holocene. A small, mid-Wisconsinan prairie dog, known only from southeastern New Mexico, is tentatively referred to the extant *C. mexicanus*. *Cynomys gunnisoni*, known from the Middle Irvingtonian to Holocene, and *C. niobriarius*, known from the Late Irvingtonian and Rancholabrean, are fossil representatives of the subgenus *Leucocrossomys*. The latter underwent geographic differentiation into northern (*C. n. churcherii*) and southern (*C. n. niobriarius*) subspecies. Two extant species, *C. parvidens* and *C. leucurus*, are derived from *C. niobriarius* and have no pre-Holocene fossil record.

Table 13. Data matrix showing distribution of 19 cranial and dental characters, and brief descriptions of states for each character. Missing characters are given as "9." Characters are as follows: 1 = On skull roof, posterior margins of premaxillae usually project (0) to the level of, (1) well posterior to the posterior margins of the nasals; 2 = Jugal angle (0) flattened, (1) weakly triangular, (2) strongly triangular; 3 = Viewed anterodorsally, anterior margin of squamosal root (0) concave, (1) flattened; 4 = Dorsal margin of occipital plate usually (0) domed, (1) moderately flattened, (2) strongly flattened; 5 = Ventral wall of infraorbital foramen usually (0) thin and horizontal, (1) robust and inclined lateroventrad from its medial end; 6 = Zygomatic plate, anterior view, (0) weakly, (1) strongly concave; 7 = Tooth rows (0) subparallel, (1) strongly convergent posteriorly; 8 = Hypsodonty of cheek teeth (0) intermediate, (1) high, (2) very high; 9 = Occlusal outline of P³ (0) circular, (1) anteriorly flattened; 10 = Ridge bounding anterior cingulum on P³ (0) low and incomplete, (1) well developed and complete; 11 = Labial portion of protoloph on M¹-M³ (0) lacks, (1) usually exhibits strong posterior expansion; 12 = M³ (0) weakly, (1) strongly elongate relative to M²; 13 = Portion of lower jaw beneath the diastema (0) slender and long, (1) relatively short and moderately or very deep; 14 = Lower cheek teeth (0) narrow, (1) moderately wide, (2) extremely wide; 15 = P₄ protolophid (0) incomplete, (1) well developed and complete; 16 = P₄ hypoconid (0) large and expanded labially, (1) reduced and not strongly expanded labially; 17 = M₃ metalophid (0) incomplete, (1) complete but low, (2) complete and high; 18 = Anterior deflection of M₃ hypoconid (0) well developed, (1) reduced but usually present, (2) absent or very weak; 19 = M₃ bridge between ectolophid and talonid platform (0) absent, (1) sometimes present and variably developed, (2) consistently present and well developed.

Taxa	Characters																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Hypo. ancestor	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9
? <i>Cynomys vetus</i>	0	1	0	9	1	0	1	9	0	0	9	0	9	9	9	9	9	9	9
<i>C. hibbardi</i>	9	9	9	9	9	9	1	0	9	9	9	1	1	1	1	0	1	0	0
<i>C. sappaensis</i>	9	9	9	9	9	1	1	1	9	9	1	1	1	1	1	0	2	0	0
<i>C. spenceri</i>	0	2	1	0	1	1	1	2	1	1	1	1	1	1	1	0	2	0	0
<i>C. ludovicianus</i>	0	2	1	0	1	1	1	2	1	1	1	1	1	1	1	0	2	0	0
<i>C. mexicanus</i>	0	2	1	0	1	1	1	2	1	1	1	1	1	1	1	0	2	0	0
<i>C. gunnisoni</i>	1	1	1	1	1	1	1	2	1	0	1	1	1	2	1	1	2	1	1
<i>C. niobrarius</i>	0	0	1	2	1	1	1	2	1	0	1	1	1	2	1	1	2	2	2
<i>C. leucurus</i>	0	0	1	2	1	1	1	2	1	0	1	1	1	2	1	1	2	2	2
<i>C. parvidens</i>	0	0	1	2	1	1	1	2	1	0	1	1	1	2	1	1	2	2	2

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APPENDIX

Referred fossil specimens, organized by taxon, age, location (alphabetically by state, county, locality), and element. Catalogue numbers followed by (?) are referred with question. Fossils referred to species known from small samples (?*Cynomys vetus*, *C. hibbardi*, *C. sappaensis*) are listed in the species accounts. Institutional abbreviations are explained in Materials and Methods. Because of the large number of fossils involved, I do not give a full description of each. Fossils are identified and grouped by basic element (e.g., L or R lower jaw). Localities marked with (*) are dated based on the prairie dogs (Goodwin, 1993), and specimens from these localities were excluded from samples of temporally defined OTUs (see Materials and Methods).

Cynomys spenceri

Sheridanian

- Kanopolis, Ellsworth Co., KS (Hibbard et al., 1978)—LM₃: UMMP 60414 Sandahl, McPherson Co., KS (Semken, 1966); L lower jaws: UMMP V40497, 50463.
- Angus, Nuckolls Co., NE (Schultz and Tanner, 1957; Martin, 1969)—palates: UNSM 33725, 33726; L lower jaws: UNSM 33706, 33715, 33898, 2068–67; R lower jaws: UNSM 33679, 33680, 33681, 33683, 33705, 33706, 33707, 33708, 33709, 33714, 33725, 33793, 33794, 2505–55.
- Angus-higher, Nuckolls Co., NE—L, R lower jaws, partial skeleton: UNSM 47723
- Prairie dog locality, Nuckolls Co., NE—R lower jaws: UNSM 47709, 47710.
- Slaton, Lubbock County, TX (Dalquest, 1967, 1988)—L maxilla: MWU 6789; R maxillae: MWU 4632, 6633, 6786; 4 L lower jaws: MWU 6652, 6786, 6787 TMM 882–4; 2 R lower jaws: MWU 6790, 6791.

Early Rancholabrean

- Mesa de Maya, Las Animas Co., CO (Hager, 1975)—L lower jaw: UWYG 6032.
- Unnamed, Clark Co., KS—L lower jaw: KUPV 13436.
- Butler Springs, Meade Co., KS—L lower jaw: UMMP 45974.
- Alma, Harlan Co, NE—L lower jaw: KUPV unnumbered (G).
- Unnamed locality in Sangamon Soil(?), Harlan Co., NE—L lower jaw: UNSM 50778.

Beaver Crossing, Seward Co., NE—L lower jaw: UNSM 2701; R lower jaw: UNSM 2702; RM₃: UNSM 2702.

Roadside Snail site, Seward Co., NE—associated L maxilla, RP₄, L lower jaw: UNSM 2713.

Sheridanian/Early Rancholabrean

Williams Farm, Rice Co., KS (Holman, 1984)—associated L, R maxillae, L, R lower jaws: UMMP V60230.

Cynomys ludovicianus

Late Rancholabrean

- Craigmile, Mills Co., IA (Rhodes, 1984)—RM₃: IOWA 46412.
- *Unnamed, Cheyenne Co., KS—partial skeleton, L, R lower jaws: KUPV 517.
- *Keiger Creek, Clark Co., KS—skull, L, R lower jaws, partial skeleton: FHSU VP-3526.
- Pyle Ranch, Clark Co., KS (Hibbard, 1944)—L maxilla, L, R lower jaws: KUPV 6710.
- Stephenson Ranch, Clark Co., KS (Hibbard, 1944)—L lower jaw: KUPV 5896.
- Duck Creek, Ellis Co., KS (Holman, 1984; date based on J. D. Stewart, pers. comm.)—partial skeleton, skull fragment, R lower jaw: KUPV unnumbered.
- *South Pit, Finney Co., KS—R lower jaw: KUPV 6909.
- *Unnamed, Finney Co., KS—L maxilla: KUPV 6818; 5L, 2R lower jaws: KUPV 6814.
- *Deer Park, Meade Co., KS (Hibbard, 1956)—L lower jaw: UMMP V60532; RM₁–M₂: UMMP 31963 (type of *Cynomys meadensis*; Deer Park fauna clearly Blancan in age but prairie dogs are intrusive; see text).
- *KU-REP-002, Republic Co., KS—R maxilla, R lower jaw fragment: KUPV 7317; L lower jaw: KUPV 7316.
- *KU-SHD-08, Sheridan Co., KS—L lower jaw: KUPV 6643.
- KU-WIL-02, Wilson Co., KS (Miller, 1978)—R lower jaw: KUPV unnumbered.
- KU-WIL-03, Wilson Co., KS—R lower jaw: KUPV 7551.
- Unnamed, Dundy Co., NE—R lower jaw: UNSM 50773.
- Citellus* zone, Lincoln Co., NE—L, R lower jaw: UNSM 30036.
- Litchfield, Sherman Co., NE (Voorhies and Corner, 1985)—L lower jaw: UNSM 88195; RP₄: UNSM 88196; RM₃: UNSM 88201.
- Dark Canyon Cave, Eddy Co., NM (Harris, 1985)—6 L lower jaws: TMM 41228-1022, -1642, -1651, -1658, -1671, -2132; 7 R lower jaws: TMM 41228-1645, -1674, -1679, -1689, -1696, -2127, UTEP 75-19.

- Howell's Ridge Cave, Grant Co., NM (Harris, 1985; Van Devender and Worthington, 1977)—L lower jaw: UTEP 32-539(?).
- U-Bar Cave, Hidalgo Co., NM (Harris, 1987, 1989)—LM₁₋₂: UTEP 5689-153-272.
- Folsom, Union Co., NM (Hay and Cook, 1930)—L lower jaw: DMNH 1248.
- UCML82009-L82010, Blaine Co., OK—2 R lower jaws: UCM 59066, 59067.
- Burnham Site, Woods Co., OK—L, R lower jaws (Burnham private collection).
- *Jackson Farm, Clay Co., TX—3 R lower jaws: TMM 30973-1.
- Clear Creek, Denton Co., TX (Slaughter and Ritchie, 1963)—isolated teeth including diagnostic LP₄: SMU 60628.
- Hickory Creek, Denton Co., TX (Slaughter et al., 1962)—R lower jaw: SMU 60296.
- Lewisville, Denton Co., TX (Slaughter et al., 1962)—palate, 2 L, 3 R lower jaws: SMU 60668.
- Lubbock Lake, Lubbock Co., TX (Johnson, 1974)—L lower jaw: TTU A5423; R lower jaw: TTU A5062.
- Ingleside, San Patricio Co., TX (Lundelius, 1972)—2 skulls: TMM 30967-850, -1014; 2 L, R maxillae: TMM 30967-834, -835; 5 L, 9 R lower jaws: TMM 30967-490, -834, -851, -933, -993.
- Foley Sands, Wichita Co., TX (Jelinek, 1960)—2 skulls: UMMP 31754, 42251; 10 L, 4 R lower jaws: UMMP 31759, 42252.
- Northwest Materials, Wichita Co., TX—3 skulls: UMMP 32360, 32361, 32362; 11 L, 8 R lower jaws: UMMP 32357.
- Laubach Cave, Williamson Co., TX (Lundelius, 1967)—fragmentary skull: TMM 40673-101; L lower jaw: TMM 41343-13.
- Bell Cave, Albany Co., WY (Zeimens and Walker, 1974)—2 L lower jaws: UWYA 4383B, 4384B; 3 R lower jaws: UWYA 4385B, 4386B, 4387B.

Cynomys cf. Cynomys mexicanus

Late Rancholabrean

- Dry Cave: Lost Valley, Eddy Co., NM (Harris, 1985, 1987)—2 L lower jaws: UTEP 1-4, -1401; 3 R lower jaws: UTEP 1-1030, -1067, -1402.

Cynomys (Cynomys) sp.

Cudahyan

- Hall Ash, Jewell Co., KS (Eshelman and Hager, 1984)—LP₄: USNM 304236.
- Burnett Ranch, Knox Co., TX (Dalquest, 1988)—M₃: MWU 12225 (not seen).

Late Pleistocene (either *Cynomys spenceri* or *C. ludovicianus*)

- Barnesville, Weld Co., CO—L lower jaw: UCM 59068.
- Unnamed, Barton Co., KS—skull: KUVF 13434.
- XI Ranch, Meade Co., KS—L lower jaw: KUVF 6476.
- Unnamed, Russell Co., KS—3 R lower jaws: KUVF 6286.
- Medicine Creek Dam Core Trench, Frontier Co., NE—palate: UNSM 50774.
- Gosper Co., NE—L lower jaw: UNSM 31250.
- UNSM-KX-102, Knox Co., NE—palate, L lower jaw: UNSM 31238.
- League Ranch, Knox Co., TX—R lower jaw: TMM 40475-5.
- Green Estates, San Patricio Co., TX—2 L lower jaws: TMM 40605-10, -16.

Cynomys gunnisoni

Cudahyan

- Hansen Bluff, Alamosa Co., CO (Rogers et al., 1985)—R maxilla, isolated teeth, associated LP₄-M₃: ADAM unnumbered.

Late Rancholabrean

- Isleta Caves, Bernalillo Co., NM (Harris, 1985)—skulls: UTEP 41-313, -314, UTEP 46-29; 23 L lower jaws: UTEP 41-316, -A2066, -A2794, UTEP 46-37, -264, -265, -267, -270, -274, -279, -290, -291, -294, -295, -300, -304, -589, -A2082, -A2083, -A3001, -A3004, -A3008, -A3014; 4 R lower jaws: UTEP 41-315, -317, -A2065, -A2346 (much of this material probably is Holocene in age).
- Burnet Cave, Eddy Co., NM (Harris, 1985)—L lower jaw: UNSM 21931; R lower jaw: UNSM 22563.
- Dark Canyon Cave, Eddy Co., NM (Harris, 1985)—2 L lower jaws: TMM 41228-1012, -1685; 6 R lower jaws: TMM 41228-1, -1011, -1655, -1691, -1694, -2132.
- Dry Cave: Animal Fair, Eddy Co., NM (Harris, 1985, 1989)—L, R maxillae: UTEP 22-1674; R lower jaw: UTEP 22-1556; 2LM₃: UTEP 22-2053, -2396.
- Hermit's Cave, Eddy Co., NM (Harris, 1985)—palate: UNSM 18972(?).
- Howell's Ridge Cave, Grant County, NM (Harris, 1985; Van Devender and Worthington, 1977)—R lower jaw: UTEP 32-548; R, L M₃: UTEP 32-531.
- U-Bar Cave, Hidalgo Co., NM (Harris, 1987, 1989)—2 L lower jaws: UTEP 5689-99-21, 5689-120-6; LM₁₋₂: UTEP 5689-109-104; 2 LM₃: UTEP 5689-78-20, 5689-78-21.

Late Pleistocene

Unnamed, Brewster Co., TX (Harris, 1985)—partial skull: UTEP 13-1 (?).

Cynomys niobrarius niobrarius

Sheridanian

Mitchell Bluff, Medicine Hat, ALT (Stalker and Churcher, 1970)—L lower jaw: ROM MB-27; L lower jaw and isolated teeth: ROM MB-135.

Sandahl, McPherson Co., KS (Semken, 1966)—L maxilla, L lower jaw: UMMP V61146; 2 R lower jaws: UMMP 45355, 50467.

Prairie dog locality, Nuckolls Co., NE—L, R maxillae: UNSM 2059-67; 5 L lower jaws: UNSM 2059-67(b), 2059-67(c), UNSM JAH-102, JAH-104, JAH-105.

Hay Springs/Rushville/Gordon, Sheridan Co., NE (Schultz and Tanner, 1957)—R maxilla: UNSM 50784; 4L lower jaws: UNSM 31377, 31380, 31388, 31389; 8R lower jaws: UMMP 41252, UNSM 21304, 31378, 31381, 31383, 31385, 31387, 50783.

Early Rancholabrean

Lindoe Bluff/Mitchell Bluff, Medicine Hat, ALT (Stalker and Churcher, 1970)—L lower jaw: ROM LB-49; RM₁₋₂, associated LP₄-M₃: ROM MB-68-476.

Mesa de Maya, Las Animas Co., CO (Hager, 1975)—LP₄: UWYG 6098.

American Falls, Power Co., ID (Pinsof, 1992)—L maxilla: IMNH 65001/16466; R maxilla: IMNH 65001/36228; 3 L lower jaws: IMNH 612/40175, 65001/36229, 78025/34276; 2 R lower jaws: IMNH 782/40183, 65001/31194.

Cragin Quarry, Meade Co., KS (Hibbard and Taylor, 1960; G. E. Schultz, 1969)—L maxilla: UMMP 35580; L lower jaw: UMMP 46045.

Alma, Harlan Co., NE—skull: KUVF unnumbered; 5 L lower jaws: KUVF unnumbered (C,D,E,F,H); 3 R lower jaws: KUVF unnumbered (A,B,I).

Sangamon Soil(?), Harlan Co., NE—L lower jaws: UNSM 50777, 50780.

Goins pocket, Lincoln Co., NE—2 L lower jaws: UNSM 50782.

Boxelder Canyon, Lincoln Co., NE—skull fragments, L, R lower jaws, postcranial elements: UNSM 30238.

Beaver Crossing, Seward Co., NE—RP₄: UNSM unnumbered.

Riddell, Saskatoon, SKT (Skwara-Woolf, 1980)—R P₄: USG VM-54.

Sheridanian/Early Rancholabrean

Unnamed, Jewell Co., KS—L lower jaw: KUVF 421. Quinn Canyon, Dawson Co., NE—R lower jaw: UNSM 30117.

Unnamed, Harlan Co., NE—skull, R lower jaw: UNSM 31249.

Unnamed, Lincoln Co., NE—L, R lower jaws: UNSM 30194.

Late Rancholabrean

Galt Island Bluff, Medicine Hat, ALTA (Stalker and Churcher, 1970)—R lower jaw, LM₁ or 2: ROM GIB-MG-19.

*Bjewelled Oriental Whitetail, Arapahoe Co., CO—2 L lower jaws: UCM 58261, 59318.

Rainbow Beach, Power Co., ID (McDonald and Anderson, 1975)—skull, L, R lower jaws, partial skeleton: IMNH 269/29107; L lower jaw: IMNH 72006/23663; R lower jaw: 72003/24645.

*South Pit, Finney Co., KS (Goodwin, 1990b)—skull, L, R lower jaws: KUVF 6908.

*Unnamed, Logan Co., KS—palate: FHSU VP-4630; 3 L lower jaws: FHSU VP-3662, VP-4631, VP-4632; R lower jaw: FHSU VP-6636.

*KU-MEA-08, Meade Co., KS—R lower jaw: KUVF 4614.

*Unnamed, Norton Co., KS—R lower jaw: FHSU VP-3183.

*KU-REP-002, Republic Co., KS—R maxilla, LP₃, R, L lower jaws: KUVF 7313; L lower jaw: KUVF 7315; R lower jaw: KUVF 7314.

KU-ROO-003, Rooks Co., KS—2 skulls: KUVF 25104, 25105; L lower jaw: KUVF 55595; 2 R lower jaws: KUVF 55596, 55597.

KU-ROO-007, Rooks Co., KS—L lower jaw: KUVF 55593; 3 R lower jaws: KUVF 60611, 63110, 63111.

Dutton Ranch No. 8, Powell Co., MT (Rasmussen, 1974)—L lower jaw: UMTG 2293.

MV 6546, Powell or Granite cos., MT—L lower jaw: UMTG 2318.

*Elm Creek, Buffalo Co., NE—6 L lower jaws: FHSU VP-3143, VP-3144, VP-3145, VP-3146, VP-3147, VP-4108; 6 R lower jaws: FHSU VP-3148, VP-3149, VP-3150, VP-3151, VP-3152, VP-4110; isolated teeth: FHSU VP-3154, VP-4111.

Smith Falls, Cherry Co., NE (Voorhies and Corner, 1985)—R maxilla: UNSM 82020; 3 L lower jaws: UNSM 82016, 82058, 82169; 2 R lower jaws: UNSM 82017, 82018; LP₄: UNSM 82063; LM₃: UNSM 82061.

Unnamed Peorian loess locality, Dawson Co., NE—R lower jaw: UNSM 30093.

Citellus zone, Dawson Co., NE—R lower jaw: UNSM 30281.

Citellus zone, Lincoln Co., NE—palate, R lower jaw, partial skeleton: UNSM 30102; R lower jaw: UNSM 30061.

Litchfield, Sherman Co., NE (Voorhies and Corner, 1985)—3 LM₃; UNSM 88197, 88199, 88200.

Roosevelt Lake, Tripp Co., SD (Green, 1960, 1963)—LP₃–M₃; SDSM 57100 (type of *C. spispiza*); LP₄; SDSM 5939; LM₃; SDSM 5940.

Natural Trap Cave, Bighorn Co., WY—L, R maxillae, L lower jaw: KUVF unnumbered.

Little Box Elder Cave, Converse Co., WY (Anderson, 1968; Indeck, 1987)—17 L, 13 R lower jaws: UCM 23608 to 23611, 23613 to 23621, 23627, 23631 to 23633, 23637, 23638, 23640, 23642, 23643, 23646, 23648, 23650.

Late Pleistocene

Nussbaum, El Paso Co., CO—palate, R lower jaw: UCM 34665.

KU-DEC-001, Decatur Co., KS—brain cast, L maxilla, R lower jaw, isolated teeth: KUVF 3968.

KU-PHI-18, Phillips Co., KS—skull: KUVF unnumbered.

KU-SHD-01, Sheridan Co., KS—L lower jaw: KUVF 12439.

Cynomys niobrarius churcheri

Late Rancholabrean

Courtney, Hand Hills, ALT (Burns and McGillivray, 1989)—3 skulls: PMA P86.11.10, P86.11.17, P89.22.2; 7 L lower jaws: PMA P86.11.10, P86.11.32, P88.20.9, P88.20.10, P88.20.30, P88.20.32, P89.22.4; R lower jaw: PMA P86.11.17.

Sinclair, Hand Hills, ALT (ibid.)—skull: PMA P75.10.1; R lower jaw: PMA P75.7.1.

Winter, Hand Hills, ALT (ibid.)—13 skulls: PMA P85.9.14, P85.9.33, P85.9.79, P85.9.97, P85.9.242, P86.3.8, P86.3.21, P86.3.25, P86.3.241, P86.3.381, P86.3.391, P86.3.516, P86.9.1; 9 L lower jaws: PMA P85.9.14, P86.3.28, P86.3.108, P86.3.143, P86.3.166, P86.3.357, P86.3.376, P86.3.450, P86.3.464; 2 R lower jaws: PMA P86.3.391, P86.9.1.

Schwalter, Wintering Hills, ALT (ibid.)—L lower jaw: PMA P87.8.2.

Cynomys (Leucocrossuromys) sp.

Sappan

Kentuck, McPherson Co., KS (Semken, 1966)—L lower jaw: UMMP 50494; RM₃: UMMP 50495 (not seen)

Sheridanian/Early Rancholabrean

Williams Farm, Rice Co., KS (Holman, 1984)—R lower jaw: FHSU VP-6931(?).

